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Sec. Research Graduate School Committee

ERRATA

p. 4, l. 18 : Replace "form" with "from"
p. 16, l. 23 : Replace "The Broken River catchment is approximately 772,386 ha" with "The Broken River catchment is approximately 760,000 ha"
p. 16, l. 25 : Replace "chapter" with "Chapter"
p. 24, l. 3 : Replace "(*Salix spp.*)" with "(*Salix* spp.)"
p. 28, l. 2 : Replace "an area of approximately 780,000 ha" with "an area of approximately 770,000 ha"
p. 43, l. 8 : Replace "data was" with "data were"
p. 51, l. 12; p. 76, l. 21; p. 80, l. 15; p. 81, l. 15; p. 158, l. 23; p. 158, last line; p.227 : Replace "Wooton" with "Wootton"
p. 65, l. 19; p.71, l. 10 : Replace "Gambusia larvae" with "Gambusia postlarvae"
p. 76, l. 3 : Replace "larval gambusia and rainbowfish" with "postlarval gambusia and larval rainbowfish"

Table 4.2 : Replace size range values of Rainbowfish, J/A, "10.1 – 34.8" with "10.1 – 55.7" and Carp gudgeons, Larvae, "2.2 – 5.9" with "2.2 – 11.9"

Recruitment Ecology of Fish in Floodplain Rivers of the Southern Murray-Darling Basin, Australia

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A thesis submitted according to the requirements for the Degree of Doctor of Philosophy at Monash University, Victoria, Australia.

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Abstract

Studies in temperate and tropical floodplain rivers have suggested that fish spawn and recruit during predictable periods of coinciding high flows and warm temperatures, allowing their larvae access to the abundant food and habitat available on the inundated floodplain environment. The importance of the flood plain for fish recruitment has been extrapolated from these studies to the native fishes of the Murray-Darling Basin. A central aspect of this 'flood recruitment model' (FRM), is the assumption that the main channel of floodplain rivers in the Basin does not support high enough densities of appropriately sized zooplankton to sustain larval fish, and that the only environment where the required densities do occur is on the inundated flood plain. However, the flood recruitment model has not been adequately tested and its generality has been questioned. Further, the recently proposed 'low flow recruitment hypothesis' (LFRH) holds that some fish can spawn and recruit during low flow periods in the main channel of floodplain rivers, without access to the flood plain, by utilising still littoral and backwater habitats that contain high densities of potential prey. However, this hypothesis has also not been tested. The aim of this thesis is to examine some of the previously untested assumptions of both the FRM and the LFRH.

Larval fish and meiofauna were sampled in the main channel of the Broken River in north-east Victoria, during the spring and summer of 1998/99. Throughout this period, water levels were within the banks of the main channel. This study demonstrated that a number of species could successfully spawn and recruit in the main channel, without flooding or access to the floodplain. As predicted in the LFRH, still littoral and backwater habitats were an important nursery habitat for a number of species.

An abundant prey source for larval fish was found to exist within the main channel, without inputs from the inundated floodplain. However, there was no relationship between the densities of prey and the habitat use of larval fish. The abundant prey source was found to occur predominantly in the epibenthic zone of the water column. Therefore, traditional methods that only sample the pelagic zone significantly underestimate the total density and diversity of fauna.

Meiofauna present in the epibenthic zone, were a significant component of the diet of all developmental stages of most species in the main channel environment, with most species consuming a wide variety of prey from the epibenthic, pelagic and surface zones. Additionally, the first feeding larvae of some species (eg. Murray cod (*Maccullochella peelii peelii*)) do not necessarily require small prey items, and those species that do (eg. Australian smelt (*Retropinna semoni*) and crimson-spotted rainbowfish (*Melanotaenia fluviatilis*)), soon altered their diets with growth to feed on a variety of larger prey items.

Larval fish sampling was conducted fortnightly on the Ovens River floodplain during the spring and summer of 1999 (non-flood year) and 2000 (flood year). Of the 19 fish species known to occur in the river, only five were collected as larvae on the flood plain. These five species also occurred as larvae during both non-flood and flood conditions. The introduced carp (*Cyprinus carpio*) was the only species to increase in larval abundance during flood conditions. The results of this study demonstrate that both the environmental conditions and life history adaptations for the direct use of the flood plain for recruitment do not necessarily occur in all floodplain rivers or for all species present in them. Rather, the direct use of the flood plain for fish recruitment is governed by a number of environmental prerequisites and the occurrence of advantageous life history characteristics of the river's fish fauna.

Based on the above findings, a more generalised conceptual model of recruitment strategies for fish in floodplain rivers is proposed. The strategies proposed in the model are based on the habitat and flow requirements for spawning and recruitment of the fish and emphasise the importance of the entire hydrological cycle and both main channel and floodplain environments in the ecology of fish in floodplain rivers.

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Statement of Originality

This thesis contains no material that has been accepted for the award of any other degree or diploma in any university or other institution, and to the best of my knowledge, contains no material previously published or written by another person, except where due reference is made in the text.

Alison Jane King

Acknowledgments

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Chapter 1: General Introduction

1.1 Recruitment Ecology

Understanding population dynamics is one of the central themes in the discipline of ecology. Fluctuations in populations are governed by changes in the rates of births and deaths, emigration and immigration (Begon *et al.* 1990). For the majority of organisms, mortality is usually very high during early life stages (eg. seeds, eggs, larvae and embryos). Typically, mortality rates decrease during adult phases, but then increase again among the older life stages (Brewer 1988). If an individual is to be represented genetically in the next generation, it must allocate time and resources to reproduction, and possess life-history strategies that maximise the chance of its progeny surviving the critical early life phase (Begon *et al.* 1990). In general ecological terms, the survival of progeny through the critical early life phase into the later life phases is known as "recruitment" (Oxford Dictionary 1993).

In fisheries ecology, recruitment is usually defined as the survival of a fish to a reference time in the life cycle, where the time can vary with species and stage (for example to the end of year 1, metamorphosis or settlement) (Trippel and Chambers 1997). The study of recruitment in fishes is often concerned with relating mechanisms, whether they are abiotic or biotic, that influence the strength of recruitment, and predict the strength of the future year class (Trippel and Chambers 1997, Miller *et al.* 1988).

The size of the recruiting year class for an annual spawner can be highly variable from one year to the next, and is widely believed to be influenced by events occurring through the early life stages (Trippel and Chambers 1997). During the early life of fishes, from embryo to larvae and into the juvenile stage, individuals undergo rapid changes in morphology, ecology, behaviour and habitat use (Fuiman and Higgs 1997, Trippel and Chambers 1997). Additionally, it is often a period of extremely variable and high natural mortality, with often greater than 99% of young fish not surviving to recruit into the adult population (Diana 1995, Houde 1997, Trippel and Chambers 1997). The key factors governing survival during early life seem to vary among species but include the supply of adequate food, predation and the influence of abiotic factors such as temperature (Houde 1997). However, whilst predation is an important factor in the survival of larvae, most

models of recruitment variability assume that food is the limiting factor and that growth rates and therefore the ability of larvae to avoid predation, are related to the availability of prey resources (Houde 1997).

Hjort (1914) and later May (1974) suggested that the greatest level of mortality during a fish's life cycle occurs through starvation, when young fish start exogenous feeding after their yolk sac is depleted. This is commonly termed the "critical period". During this period, it is assumed that larvae must encounter high densities of appropriately sized prey to maximise their chance of survival. Miller *et al.* (1988) have suggested, however, that larger larvae are not as vulnerable during this critical first feeding period as smaller larvae. Regardless of whether or not a critical period for larval survival exists, the availability of food is generally accepted as a limiting factor in the growth and survival of individuals and has been widely incorporated into stock-recruitment models (Cushing 1990, Jobling 1995, Houde 1997). Therefore, it may be expected that the rate of larval growth and survival, and subsequent recruitment, would be related to the amount of prey available when the peak number of fish larvae occur.

The relationship between the timing of the occurrence of fish larvae and their prey forms the basis of the match/mismatch hypothesis proposed by Cushing (1990), which was constructed for recruitment of temperate marine fish. It proposes that larval growth and survival will depend on the degree of temporal overlap between the spawning season and plankton production (Figure 1.1) and extends the importance of the critical feeding period (Hjort 1914, May 1974) to all larval stages (Cushing 1990). The hypothesis proposes that strong recruitment and year class strength will occur when spawning and peak abundance of larvae overlaps with the peak production of prey, and thus causes a 'match' (Figure 1.1a). On the other hand, poor recruitment will occur when the spawning season does not significantly overlap with the peak production of prey, and thus causes a 'mismatch' (Figure 1.1b).

The underlying assumptions of the match/mismatch hypothesis are that the timing of spawning and therefore the peak abundance of larvae is fairly constant from year to year, while the timing of the annual peak in production of the plankton varies, and is related to environmental conditions such as water temperature (Cushing 1990). The hypothesis has

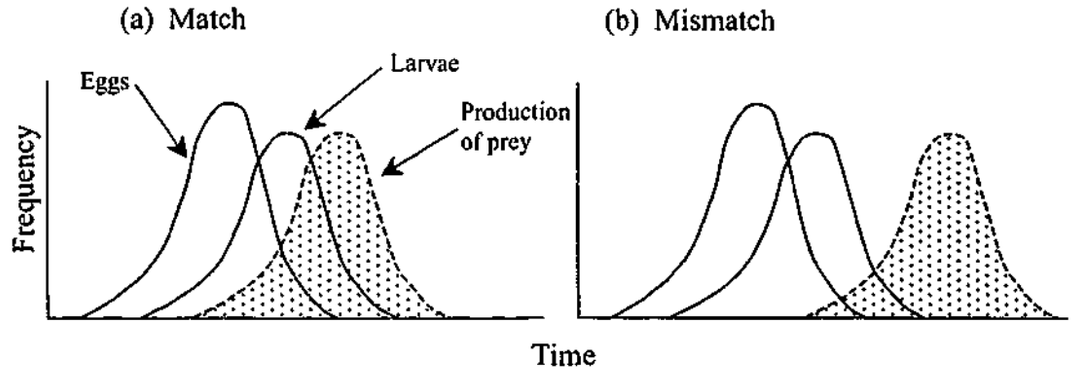


Figure 1.1: Conceptual model of the match/mismatch hypothesis (adapted from Cushing 1990). The production of eggs and larval fish, and larval food (prey) are shown as distributions in time. The (a) match or (b) mismatch is represented by the overlap in time between the production of fish larvae and that of their food.

been tested and supported in number of studies in marine systems (eg. Cushing 1990, Fortier and Gagné 1990, Gotceitas *et al.* 1996, Brander *et al.* 2001). Although not derived directly from the match/mismatch hypothesis, an analogous model of the relationship between the strength of fish recruitment, the abundance of larvae and their prey is proposed in the 'flood pulse concept' (FPC) for floodplain rivers (Junk *et al.* 1989).

1.2 Fish Recruitment in Floodplain Rivers

The FPC is one of the major models that describes the production of animal biomass in floodplain rivers (Junk *et al.* 1989). The FPC proposes that "in unaltered large river systems with flood plains in the temperate, subtropical, or tropical belt, the overwhelming bulk of the riverine animal biomass derives directly or indirectly from production within the flood plains and not from downstream transport of organic matter produced elsewhere in the basin" (Junk *et al.* 1989). The FPC is considered as more appropriate in large floodplain rivers than the 'river continuum concept' (Vannote *et al.* 1980), which emphasised only the longitudinal transport of organic matter. In contrast, Thorp and Delong (1994), in the 'riverine productivity model', hypothesise that the major source of organic matter assimilated by animals in large rivers, is derived from local autochthonous production (including phytoplankton, benthic algae, macrophytes and mosses) or direct inputs form the riparian zone. Despite continuing debate as to the origins of organic matter fuelling food webs in large floodplain rivers (Thorp *et al.* 1998, Gutreuter *et al.* 1999), currently the most widely accepted model is the FPC.

For riverine fishes, the FPC emphasises the role of floodplain inundation, providing a spawning cue for some fishes and an abundance of food and habitat for all life stages, including larvae (Junk *et al.* 1989, Bayley 1991). Flooding is the major cue for breeding of most tropical riverine fishes, where marked seasonal differences in temperature do not occur (Welcomme 1985). In temperate systems, however, the FPC stresses the importance of the coincidence of high temperatures and high flows for the successful utilisation of the flood plain by fishes for spawning and recruitment (Junk *et al.* 1989). Thus, good recruitment should result when spawning occurs when the rise of water levels and temperature are coupled. Conversely, poor recruitment will occur when water level and temperature rises are decoupled, such as if the flood occurs outside spring or summer. The FPC has stimulated a range of studies that have, in general, supported its predictions across temperate to tropical floodplain rivers throughout the world (Bayley 1995, Sparks 1995,

Galat *et al.* 1998, Sparks *et al.* 1998, Gutreuter *et al.* 1999). However, a number of hydrological factors, such as the predictability, duration, timing and magnitude of the flood pulse, have also been recognised as important in the response and production of fishes during flooding (Bayley 1991, Poff *et al.* 1997, Galat *et al.* 1998, Sparks *et al.* 1998, Tockner *et al.* 2000, Fontenot *et al.* 2001).

Despite floodplain inundation being accepted as the major fish recruitment model for floodplain rivers, a number of studies have documented the use of in-channel habitats and off-channel lakes (billabongs) for rearing of fish larvae and successful recruitment in major rivers throughout the world. In the main channel environment, larvae have generally been found to utilise shallow, still littoral areas, backwaters and embayments as nursery habitats (Moore and Gregory 1988a, Schiemer and Spindler 1989, Haines and Tyus 1990, Tyus 1991, Sempeski and Gaudin 1995, Wintersberger 1996, Watkins *et al.* 1997). These are thought to be ideal nursery habitats, as they provide areas of refuge from high water velocity and predators and can contain higher densities of larval prey than main channel habitats (Schlosser 1987, Harvey 1991, Eklöv *et al.* 1994, Thorp *et al.* 1994, Mann and Bass 1997). In addition, fish reproduction and recruitment can also occur in the mosaic of permanent and temporary wetlands, lakes and anabranches on the flood plain, without the occurrence of floods or connection to the main channel (eg. Copp 1989b, Copp *et al.* 1994, Turner *et al.* 1994).

Whilst applicable to floodplain rivers elsewhere, two complementary fish recruitment models have recently emerged for Australian floodplain rivers. The first, termed the 'flood recruitment model' by Harris and Gehrke (1994), was derived from both the match/mismatch hypothesis (Cushing 1990) and the FPC (Junk *et al.* 1989), and proposes that enhanced fish recruitment and resulting strong year classes, are linked to flooding cycles. The second model, the 'low flow recruitment hypothesis' (Humphries *et al.* 1999), proposes that some fish can successfully recruit within the main channel environment of floodplain rivers during low flow periods, by utilising food-rich habitats such as backwaters. Both of these hypotheses have stemmed from studies and observations in the Murray-Darling Basin, in which regional climatic conditions vary greatly and whose rivers are characterised by highly variable flow patterns (Puckridge *et al.* 1988).

1.3 The Murray-Darling Basin

Description

The Murray-Darling Basin occurs in south-eastern Australia, between the latitudes 24 – 37° S and longitudes 138 – 153° E (Figure 1.2). The Basin drains an area of just over 1 million km^2, or 14% of Australia, with the Murray and Darling Rivers alone having a combined length of 5,500 river km (Walker and Thoms 1993). The headwater streams of the Murray-Darling Basin generally rise in the mountains of the Great Dividing Range, and flow westward as large lowland rivers on low relief flood plains, and eventually enter the sea near Adelaide. Much of the Basin is in semi-arid to arid climatic regions, where rainfall is low and evaporation rates are high. Despite the size of the Basin, the mean annual discharge to the sea is only 10,090 GL (Maheshwari *et al.* 1995); as a comparison, this flow would pass through the Amazon River in less than one day (Young *et al.* 2001). The Basin has 24 major rivers that are an important source of fresh water for the Basin's flora and fauna, domestic consumption, agricultural production and industry. The region generates approximately 40% of the national income derived from agriculture and grazing, and supports a quarter of the nations cattle herd, half of the sheep flock, half of the cropland and almost three quarters of its irrigated land (Crabb 1997). Irrigated floodplain agriculture alone, which yields more than $A10 billion annually, accounts for 90% of the annual water consumption of the Basin (Thoms and Sheldon 2000). The Basin extends over five states and territories, with water resource issues principally managed by two across-government organisations, the Murray-Darling Basin Ministerial Council and the Murray-Darling Basin Commission.

Climatic conditions vary greatly throughout the Murray-Darling Basin, and can be broadly placed into three climatic regions (Nix and Kalma 1982, Young 2001). These range from the cool, humid, mountainous regions of the Eastern Highlands, to the warm and dry Murray-Murrumbidgee lowlands where rainfall predominantly occurs in winter, to the northern Darling River basin, where it is warmer and drier, but is dominated by summer rainfall cycles. The Basin's climate is also characterised by extremely variable rainfall from year to year, leading to highly variable river flows, including severe flood and drought cycles.

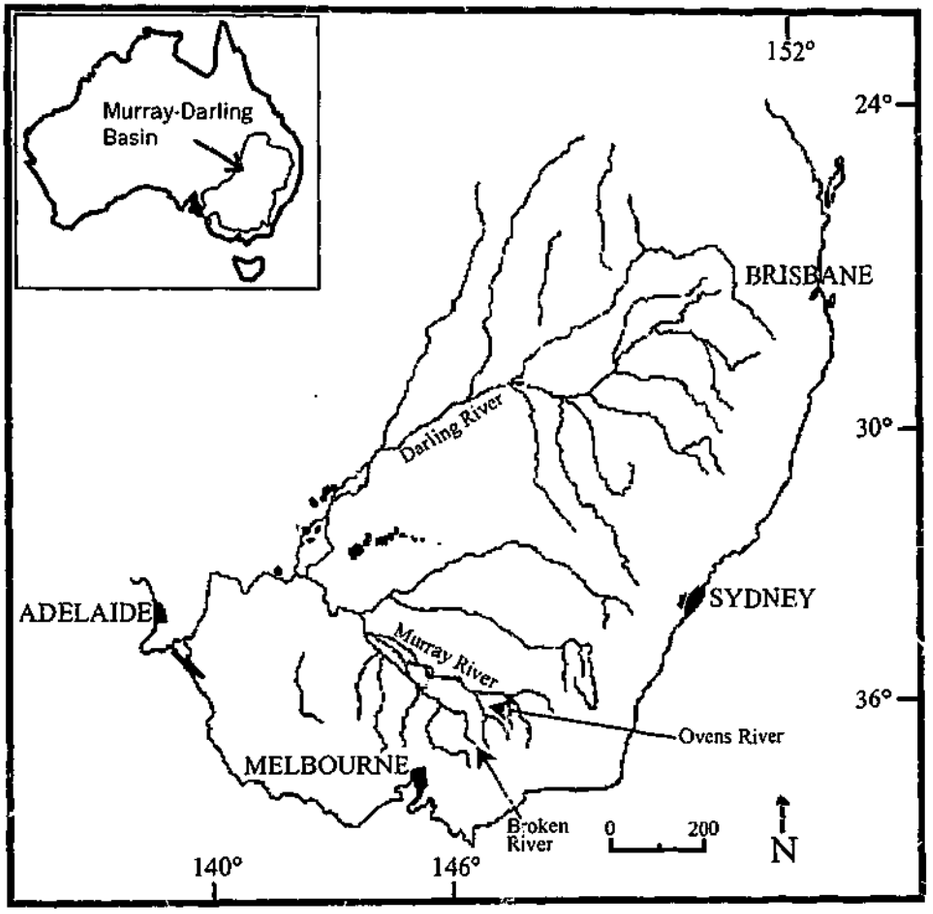


Figure 1.2: Map of the Murray-Darling Basin.

This extreme variability of river flows encouraged the regulation and development of most of the Basin's large rivers, with many now predominantly used as supply channels for irrigation water, controlled by large upstream storages and numerous downstream weirs and lochs. Regulation of the Basin's rivers has resulted in nearly two thirds of the water that would have originally reached the sea, now being diverted for predominantly off-stream agricultural use (Close 1990, Crabb 1997). River regulation has caused other serious effects such as a reduced amount of water in the channel downstream of major irrigation areas, reversal of seasonality of flows, reduced flood flows but increased flows during droughts, depressed water temperatures downstream of dams, instream barriers, and reduced frequency of floodplain inundations (Walker 1979, Close 1990, Walker and Thoms 1993, Crabb 1997). These changes to the flow have had major detrimental impact on the ecology of the rivers and are widely considered the main cause of the degradation of the Basin's aquatic ecosystems (Cadwallader 1978, Walker 1979, Cadwallader and Lawrence 1990, Walker and Thoms 1993).

Fish fauna of the Murray-Darling Basin

The Murray-Darling Basin contains only 26 species of fish, from 12 families, that spend their entire lives in freshwater and, of these, 10 are endemic to the system (Cadwallader and Lawrence 1990). A further 11 species have been introduced into the Basin; some such as carp (*Cyprinus carpio*) and gambusia (*Gambusia holbrooki*), are widespread and abundant. The high natural flow variability and Australia's geographic isolation from the rest of the world's continents, is thought to have contributed to the relatively low diversity of native fishes in the Basin (Lake 1971, Allen 1989, Lloyd *et al.* 1989). However, considering the region's aridity and the resulting limited availability of aquatic habitats, it has been argued that the Basin's fish fauna could be viewed as relatively rich, especially if species richness to drainage size comparisons are made over similar latitude and climatic regions (Lake 1995, Gehrke and Harris 2000).

Although the Basin's native fish fauna is comprised of relatively few species, the fauna exhibits a diverse array of sizes, habitat preferences and life history styles. Sizes range from small forage species that rarely exceed 50 mm in length and 2 g in weight, such as Australian smelt (*Retropinna semoni*), up to species such as Murray cod (*Maccullochella peelii peelii*) that has been reported to grow to 2 m in length and can weigh in excess of 100 kg (McDowall 1996). Adult native fish are known to utilise a variety of habitat types

from deep pools and shallow littoral habitats in the main channel of rivers, to temporary and permanent floodplain habitats such as billabongs (or oxbow lakes) and upland creeks and rivers.

Humphries *et al.* (1999) proposed that native fishes of the Basin could be classified into four life history styles (Table 1.1), based primarily on characteristics of their spawning, larval size and development, and the time to first feeding. This life history classification is similar to that proposed by Winemiller (1992) and Winemiller and Rose (1992). The categorisation used by Winemiller (1992) defines three strategies, that include: (i) 'equilibrium' (similar to mode 1 fishes of Humphries *et al.* (1999)), with traits such as large eggs, parental care of eggs and young, small clutches and individuals that are well developed at independence; (ii) 'periodic' (similar to mode 2 fishes of Humphries *et al.* (1999)), where individuals have large clutches, small eggs and tend to be highly migratory, and (iii) 'opportunistic' (similar to mode 3a and 3b fishes of Humphries *et al.* (1999)), where individuals have small body sizes and rapid larval growth rates.

However, whilst the diversity of sizes, habitat preferences and life history styles are quite high within the Basin's fish fauna, the diversity of trophic feeding guilds is low, with the majority of species being opportunistic carnivores feeding on fish, macro- and microinvertebrates (McDowall 1996, Kennard *et al.* 2001, Schiller and Harris 2001). None of the native species is totally piscivorous and only a few species are thought to be either detritivores or omnivores.

Whilst as yet no species has become extinct in the Basin, 19 species are considered as threatened or rare (Schiller and Harris 2001), and a number of regional extinctions have also occurred (Lloyd and Walker 1986). Since European settlement, the Basin's fish fauna has undergone dramatic declines in both abundance and distribution (Cadwallader 1978, Cadwallader and Lawrence 1990, Faragher and Harris 1994). The declines in abundance of all native species in the Basin are attributed to a number of factors such as altered flow regimes, habitat destruction (for example, large woody debris removal), water quality declines (for example, siltation and salinisation), overfishing, and predation and competition by introduced species (Cadwallader 1978, Cadwallader and Lawrence 1990, Koehn and O'Connor 1990a). The effects of river regulation are thought to have had the most dramatic impact on native fish, including the removal of reproductive cues, barriers

to movements and migrations, reductions in aquatic vegetation and deeper pool habitats, and the reduction of access to the flood plain (Cadwallader 1978, Cadwallader and Lawrence 1990, Koehn and O'Connor 1990a, Schiller and Harris 2001).

Table 1.1: Life history styles for several Murray-Darling Basin fishes. Source: Humphries *et al.* (1999).

Variable	Mode 1	Mode 2	Mode 3a	Mode 3b
Duration of spawning period	Short	Variable	Long	Short
Spawning style	Single spawning, approx. same time each year	Single spawning, can delay	Protracted, serial or repeat	Single spawning
Spawning time	Oct – Dec	Oct – Mar	Sept – Mar	Late winter or summer
Cues for spawning	Circannual and min. temperature	Rising water levels and critical temperature	Uncertain	Uncertain
Number of eggs	1000s – 10 000s	100 000s	100s – 1000s	100s – 1000s
Type of egg	Demersal	Semi-buoyant or buoyant	Planktonic or demersal	Planktonic or demersal
Parental care of embryo/larva	Yes	No	No	No
Incubation period	10+ days	Hours	< 10 days	< 10 days
Size at hatching	6 – 9 mm	3 – 6 mm	3 – 4 mm	2 – 7 mm
Time to first feeding	20 days	5 days	3 days	3 days
Development of embryo/larva at first feeding	Advanced, large gape, well developed fins, highly mobile	Undeveloped, small gape, limited mobility	Undeveloped small gape, limited mobility	Undeveloped, small gape, limited mobility
Examples of species	Murray cod, trout cod, freshwater catfish, river blackfish	Golden perch, silver perch	Australian smelt, flatheaded gudgeon	Carp gudgeons, *Galaxias olidus*, *G. rostratus*, crimson-spotted rainbowfish, southern pygmy perch

1.4 Fish Recruitment in the Murray-Darling Basin

The flood recruitment model

The successful recruitment of native fishes in the Murray-Darling Basin is widely thought to be linked to periods of floodplain inundation (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992, Lloyd *et al.* 1994, Schiller and Harris 2001). This has stemmed, in part, from the extrapolation of overseas models in river floodplain systems such as the FPC (Welcomme 1985, Junk *et al.* 1989) and early aquaculture studies on the breeding biology of a few native species (Lake 1967a & b, Llewellyn 1971, 1973, 1974). In the proposed model, termed the 'flood recruitment model' (FRM) by Harris and Gehrke (1994), flooding enhances recruitment by directly stimulating spawning for some species and indirectly enhancing recruitment of both flood cued and non-flood cued species by providing abundant food and habitats for larvae to develop on the inundated flood plain (Geddes and Puckridge 1988, Lloyd *et al.* 1989, Gehrke 1991, Harris and Gehrke 1994, Lloyd *et al.* 1994, Schiller and Harris 2001). The model consists of four stages; (i) inundation of floodplain habitats releases nutrients; (ii) which then triggers an increase in primary production, resulting in plankton blooms; (iii) sexually mature fish, eggs or larvae then enter the flood plain and utilise the abundant prey; and (iv) receding waters transport larvae or juveniles back into permanent water bodies (Gehrke 1993).

One pathway of the FRM proposes that floods provide direct benefits to flood-cued species, such as golden perch (*Macquaria ambigua*), by actively stimulating spawning. In early aquaculture breeding trials of native fish, Lake (1967a) established that golden perch and silver perch (*Bidyanus bidyanus*), spawned when water temperatures were above 23°C, provided that there was an accompanying rise in water level. Other studies have then linked flooding to strong year classes of golden perch, suggesting that poor recruitment occurs in low flow years (Mackay 1973, Cadwallader 1978, Cadwallader and Lawrence 1990). Reid *et al.* (1997) also found a strong relationship between the commercial catches of native species and flow height, but suggested that it was difficult to ascertain whether the relationship was due to the increased catchability or increased recruitment. In contrast, however, Mallen-Cooper *et al.* (1995) found that strong year classes of golden and silver perch in the Murray River were associated with in-channel spring flows and not flood years. To date, the only known collection of golden perch larvae in the wild is of a few

individuals during a low flow period in the Broken River, Victoria (Humphries *et al.* in press).

For species in the Basin that do not require floods for spawning, the FRM postulates that floods may enhance larval survival and recruitment by providing a food-rich environment, suitable for the rearing of their larvae (Harris and Gehrke 1994, Schiller and Harris 2001). This aspect of the model is similar to the match/mismatch hypothesis (Cushing 1990) and that proposed for temperate fishes in the FPC (Junk *et al.* 1989), in that good recruitment will only occur when the timing of the peak production of fish larvae overlaps with the peak production of their prey. One of the main tenets of the FRM is that the main channel of floodplain rivers does not provide high enough densities of suitable prey to sustain larvae, and that the only environment where the required densities do occur is on the inundated flood plain (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992). A number of studies in Australia have demonstrated that suitable densities of potential prey do occur in floodplain habitats during both high and low flow periods (Crome 1986, Crome and Carpenter 1988, Tan and Shiel 1993). However, whilst only a few Australian studies have examined the densities of pelagic zooplankton in the main channel of floodplain rivers, the densities have ranged from quite low numbers in the Murray and Darling Rivers (< 150 individuals L^{-1}, Shiel *et al.* 1982, Shiel 1985) to fairly high densities in the Hawkesbury-Nepean River (< 803 individuals L^{-1}, Kobayashi *et al.* 1998).

Despite the common assumption that the larvae of all native species require dense blooms of small prey items such as rotifers and small crustaceans (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989), the diets of larvae of only a few native species have been studied, with only one of these conducted in the wild, albeit an off-channel billabong (Gehrke 1992). In addition, aquaculture studies have found that the diets of first feeding larvae of trout cod (*Maccullochella macquariensis*) and Murray cod are composed of relatively large items such as copepods, cladocerans, chironomid larvae and corixids (Ingram and Rimmer 1992, Rowland 1992).

To date, no published studies have documented larvae of any native species occurring on the flood plain during flood periods in the Basin. Although recognising the lack of empirical evidence of the importance of the inundated flood plain for larvae, Gehrke

(1990a & b, 1991) and Gehrke *et al.* (1993) conducted a series of experiments aimed at determining the suitability of the flood plain for fish larvae. The results suggested that golden perch larvae actively avoided artificial floodplain areas, due to poor water quality conditions such as low dissolved oxygen concentrations (Gehrke 1990a, 1991). Further experiments suggested that although golden perch were attracted to the leachate of the leaves of river red gum (*Eucalyptus camaldulensis*), a common riparian tree (Gehrke 1990b), the leachate could easily be in lethal levels in the natural environment (Gehrke *et al.* 1993).

Therefore, despite the perceived importance of the flood plain to the sustainability of the Basin's fishes, especially within the management literature, a number of the assumptions supporting the model lack thorough scientific evidence and have been recently questioned as to their validity and generalisation across the entire Basin (Humphries *et al.* 1999).

The low flow recruitment hypothesis

Whilst the importance of the flood plain for fish recruitment in the Basin's rivers has received considerable attention, the role of the main channel environment has received comparatively little consideration. Recent work in two floodplain rivers in the southern region of the Basin, has demonstrated that larvae of a number of native species occur in the main channel environment (Humphries and Lake 2000, Humphries *et al.* in press). Indeed, for species such as flathead gudgeon (*Philypnodon grandiceps*), Australian smelt, crimson-spotted rainbowfish (*Melanotaenia fluviatilis*) and three species of carp gudgeons (*Hypseleotris spp.*), their larvae are known to occur and recruit in the main channel during the summer low flow period, when the probability of flooding is low (Humphries *et al.* in press).

These findings led to the construction of the 'low flow recruitment hypothesis' (LFRH), that postulates that some species may take advantage of the extended and relatively predictable low flow period to spawn, because of high concentrations of prey occurring in main channel habitats such as backwaters, pools and other still areas (Humphries *et al.* 1999). The LFRH suggests that as flows decrease and water temperatures warm over late spring and summer, the smaller volume of warm water concentrates potential prey to densities sufficient for the survival of fish larvae. Further, it proposes that the potential prey items may also include fauna that occur on or near the sediment surface (epibenthic),

such as cladocerans, copepods and their nauplii, ostracods and small first instar insect larvae, and that this fauna is generally inadequately sampled using conventional zooplankton sampling techniques.

A number of overseas studies have demonstrated that as zooplankton biomass is known to be positively correlated with water residence time (Basu and Pick 1996) and temperature (Thorp *et al.* 1994), and negatively correlated with flow (Pace *et al.* 1992, Thorp *et al.* 1994), the greatest densities of zooplankton in the main channel of large rivers will occur during the lowest flow periods, which generally occur in summer (Ferrari *et al.* 1989, Pace *et al.* 1992, Thorp *et al.* 1994, Basu and Pick 1996). The increased water residence time in some non-flowing habitat patches, such as backwaters, bays, eddies and pools, may allow higher densities of zooplankton to occur within the main channel of rivers (Thorp *et al.* 1994, Basu and Pick 1996, Reckendorfer *et al.* 1999, Reynolds 2000). Although a few studies have examined the densities of microfauna within the main channel of the Basin's rivers (Shiel *et al.* 1982, Shiel 1985), neither the densities of microfauna within discrete main channel habitats nor the importance of the epibenthic zone as a contributor to the overall densities of microfauna has been studied.

Additionally, whilst still or slow flowing habitats, such as backwaters, embayments, littoral areas and pools, are known to be important nursery areas for fish larvae in overseas rivers (Moore and Gregory 1988a, Schiemer and Spindler 1989, Haines and Tyus 1990, Tyus 1991, Sempeski and Gaudin 1995, Wintersberger 1996, Watkins *et al.* 1997), the ontogenetic habitat requirements of the Basin's fish species has not been established.

1.5 Aims of the Thesis

Despite the construction of two recruitment models for the Basin's fish fauna, and the widespread acceptance of the applicability of the FRM for the management of the Basin's rivers, there is little scientific evidence to support a number of the major assumptions in both models. For example, few studies have demonstrated the use of the main channel or floodplain habitats for fish recruitment or their nursery habitat preferences in either of these environments. Additionally, the diets of native fish through ontogeny are poorly understood. Finally, only a few studies have sampled the main channel environment of floodplain rivers in the Basin for zooplankton and no study has compared the densities of potential prey available in the pelagic and epibenthic zones. There is also increasing speculation as to the applicability of the models to all environmental conditions and to all species within the Basin (Humphries *et al.* 1999).

Therefore, the general aim of this thesis is to assess some of the previously untested assumptions of both the FRM and the LFRH for Murray-Darling Basin fishes. Specifically, it aims to:

1. Describe and evaluate a new electrofishing method for sampling larval and juvenile fish in lotic environments (Chapter 3),
2. Establish which species utilise the main channel of a floodplain river for spawning and recruitment, and determine their habitat preferences throughout ontogeny (Chapter 4),
3. Describe the ontogenetic dietary composition and dietary overlaps of species that utilise the main channel for recruitment (Chapter 5),
4. Establish whether suitable densities of potential larval fish prey items occur in the main channel without flood plain connection occurring, and determine whether a greater density of potential prey items occur in the epibenthic zone compared to the pelagic zone (Chapter 6),
5. Establish which species utilise the flood plain as larvae during connection and isolation from the main channel in flood and non-flood years (Chapter 7).

Chapter 2: Study Area Description

2.1 Study Region

The present study was conducted in two rivers in the south-east region of the Murray-Darling Basin, Australia. The Broken and Ovens Rivers are situated in the north-east region of Victoria, flowing generally north from the Great Dividing Range and eventually into the Murray River (Figure 2.1). These two rivers were chosen for the study for a number of reasons including, their relatively unregulated nature (Humphries and Lake 2000, Cottingham *et al.* 2001a and b), the rivers are known to support a high diversity of native fish species in common to both and the aquatic fauna of both have been reasonably well studied. The Broken River was used to study the habitat use of larvae and juvenile/adult fish and the density and distribution of their potential prey within the main channel environment (Chapters 4 and 6). The use of floodplain habitats by larvae and juveniles was conducted in the Ovens River (Chapter 7). Neither river was suitable for both the main channel and floodplain sampling, as (i) flooding in the Broken River is unpredictable and because the study was conducted during an extended dry period when a flood of sufficient magnitude and duration was unlikely to occur, and (ii) that the size and morphology of the main channel in the Ovens River meant that stratified habitat sampling would have been extremely time and labour intensive and may have precluded the sampling of some habitat types.

2.2 The Broken River

The Broken River rises on the northern-facing slopes of the Great Dividing Range in the Alpine National Park in Victoria. The river flows north, then west past the town of Benalla, and then discharges into the Goulburn River, a tributary of the Murray River, near Shepparton (Figure 2.2). The Broken River catchment is approximately 772,386 ha, and the river has an approximate mean annual discharge of 236,000 ML (DWR 1989a). The catchment includes Broken Creek, which diverges from the Broken River at Casey's weir, and flows north into the Murray River. The study described in chapter 4 was conducted at three sites, 'lower', 'middle' and 'upper', in the lowland reaches of the Broken River, downstream of Benalla (Figure 2.2).

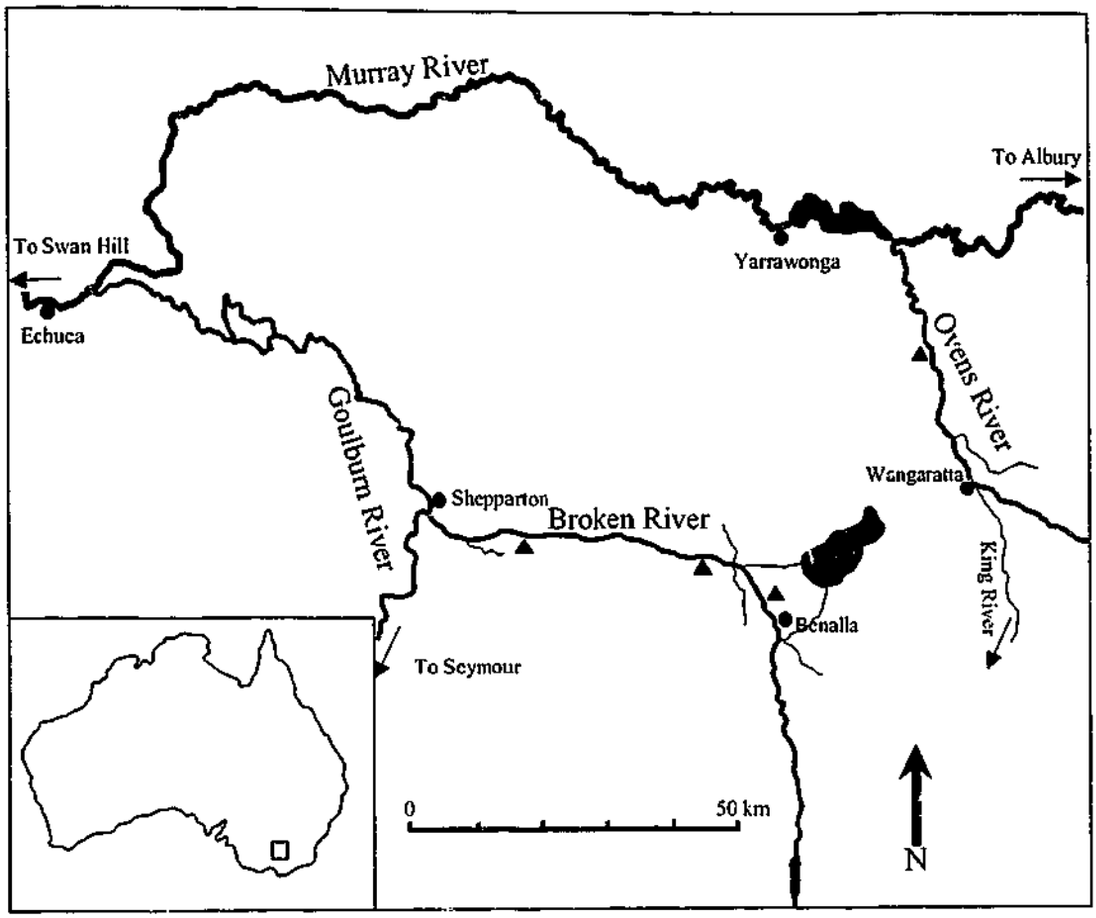


Figure 2.1: Map of study region. Inset: Map of mainland Australia with study region highlighted. ▲ = sampling site.

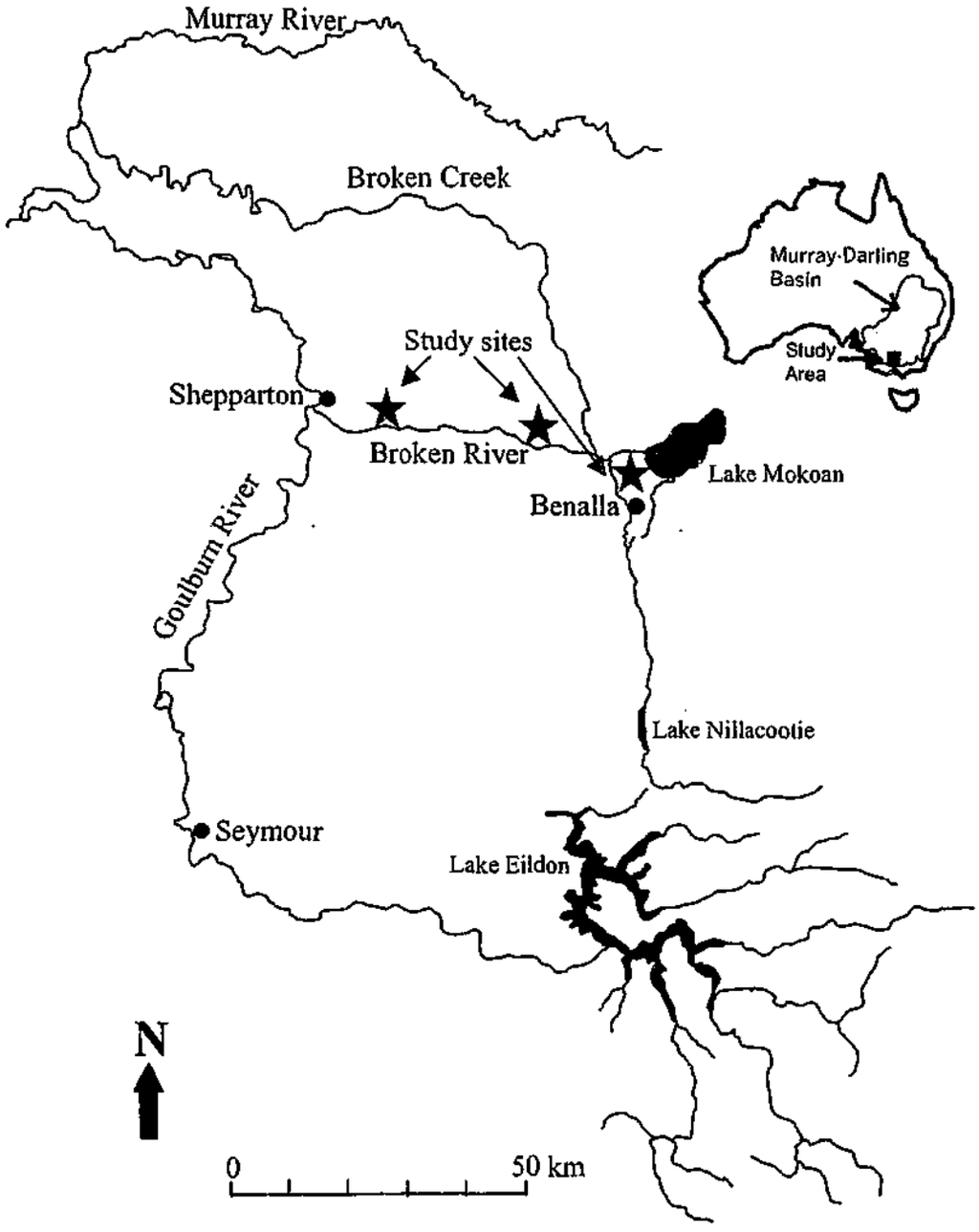


Figure 2.2: Map of Goulburn-Broken River catchment. ★ = study site.

Brief history and land use

Although the explorers Hamilton Hume and William Hovell crossed the Broken River in 1824, most early descriptions of the land were left to other travellers, who described a region of extensive grassy, treeless plains with open woodlands to the north of the catchment. Squatters and graziers settled the land soon after the arrival of the explorers and travellers (DWR 1989b).

Most of the Broken River catchment has now been cleared for agriculture, consisting mainly of mixed cereal and livestock farming (Table 2.1). The lower reaches of the catchment are also part of the Murray Valley Irrigation district, producing mainly fruit, dairy and livestock (GWQWG 1996). The remaining forest areas are primarily in the steeper country in the south, the Warby Ranges to the east and along the Murray River in the north. The population of the Goulburn-Broken catchment is approximately 250,000 (GWQWG 1996).

Table 2.1: Major land use types in the Broken River catchment. Source: GWQWG (1996).

Land use type	Area (ha)	% of total
Native vegetation (forest)	111650	14.7
General agriculture (dryland)	532070	69.9
Intensive agriculture (irrigation)	99330	13.1
Plantation	16940	2.2
Urban	770	0.1
Total	**760760**	

Geomorphological character

The steeper upper reaches of the Broken River catchment consist primarily of sedimentary rocks and granite intrusions. The river then flows along an alluvial flood plain, through low foothills down to the broad alluvial plains of the Murray Basin Riverine Plain (DWR 1989a). The Warby Range, a granite formation, forms the north-east boundary of the catchment.

The geomorphic character of the river has probably not altered since flow regulation, as the larger flow events in the system have not been affected. However, "river improvement" works that occurred in the past, such as the removal of snags, channel works and the

construction of levee banks, are likely to have contributed to bank erosion and reduced habitat conditions in the main channel (Cottingham *et al.* 2001a).

Climate

Climate varies considerably within the Broken River catchment, with the southern part of the catchment receiving an average annual rainfall of 1270 mm and the northern region receiving 470 mm. The high mountain slopes receive regular rainfall and light snowfalls in winter, while the plains region experiences hot summers and mild winters.

Benalla, the nearest regional centre to the sites used in this study, experiences mild winters (mean daily minimum and maximum, 3.2 – 14.6 °C) and warm summers (12.9 – 31.0 °C) (Figure 2.3a) (Bureau of Meteorology). Rainfall in the region is approximately 674 mm annually, with maximum falls between June and August, and minimum falls between December and March (Figure 2.3b) (Bureau of Meteorology).

Hydrology and water storages

The natural flow of the river varies considerably from year to year, with large seasonal variations from winter flooding to very low summer flows. The three months from July to September account for over half of the average annual flow (DWR 1989b). Annual flow has ranged from only 5,000 ML in the drought year of 1943, to more than 1,000,000 ML in the two flood years of 1917 and 1956 (DWR 1989b). Records from 1885 to 1960 show that the river ceased to flow for at least one month during summer or autumn in 23 out of the 75 years (Rundle and Rowe 1974). Flooding occurs approximately one in every four years, primarily after continuous heavy rainfall in the upper catchment, usually between late winter and early spring. Floodplain inundation in the lowland reaches occurs at approximately 21,400 ML day^{-1} (B. Dubkovski, Theiss Environmental Services, pers. comm.). During the main study period, from October 1998 to the end of January 1999, one significant rise in flow did occur but did not reach minor flood levels and remained confined to the banks of the main channel (Figure 2.4).

There are two major storages within the Broken River catchment (Figure 2.2). Lake Nillahcootie is on the Broken River in the south of the catchment, and was constructed in 1972. The storage provides a reliable water supply for stock and domestic requirements,

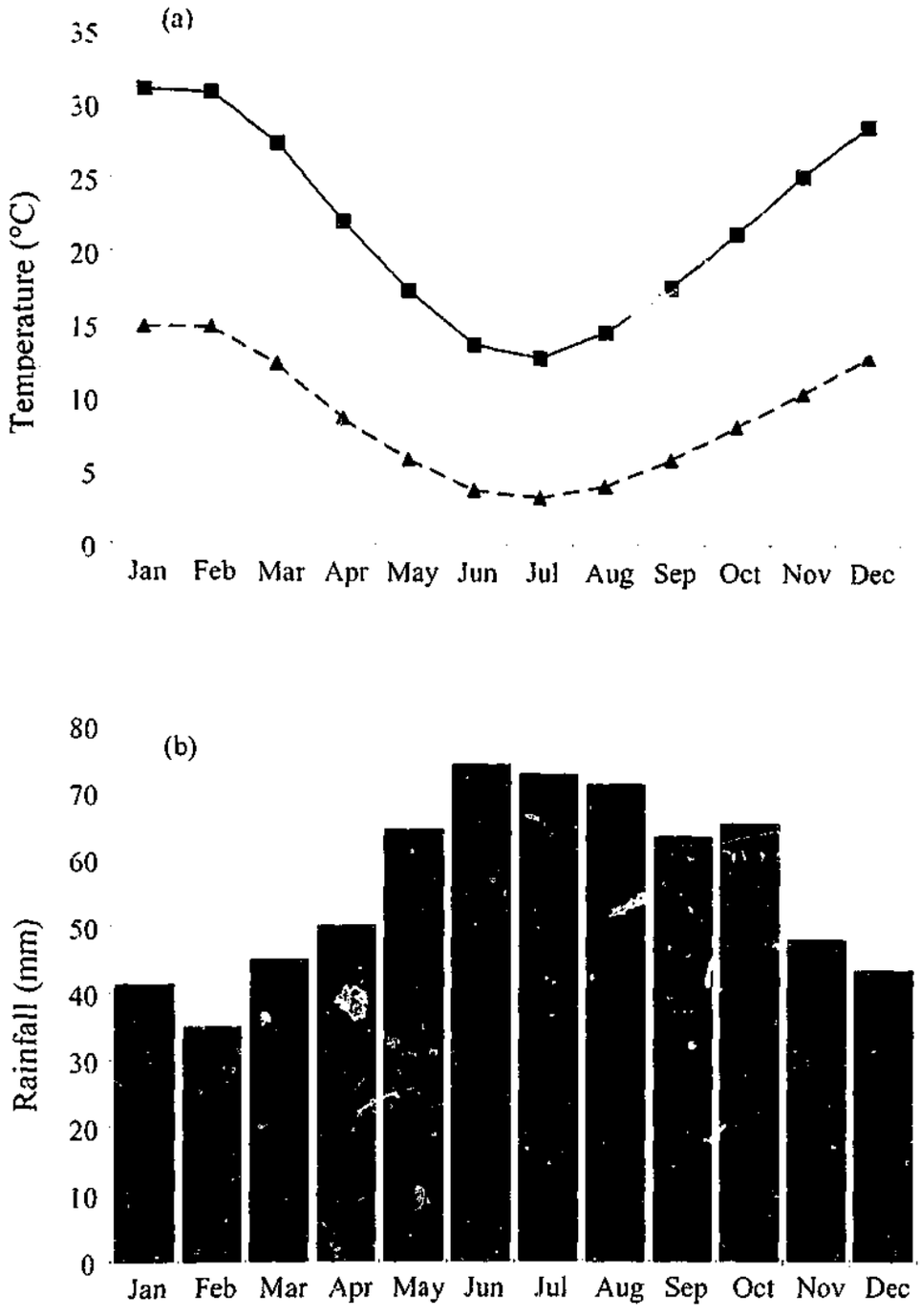


Figure 2.3: (a) Monthly mean maximum (—■—) and minimum (--▲--) air temperatures and (b) monthly mean rainfall at Benalla. Source: Bureau of Meteorology.

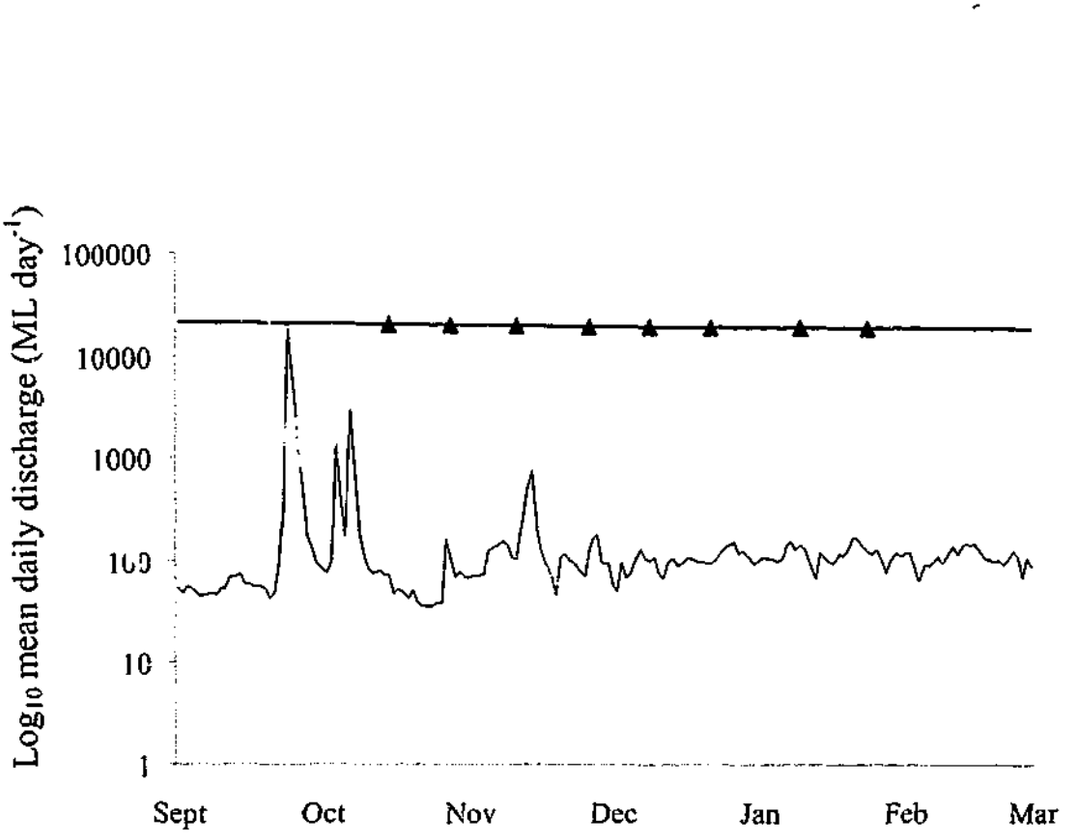


Figure 2.4: Log_{10} mean daily discharge (ML day^{-1}) (thin solid line) for the Broken River at Casey's Weir between 1 September 1998 and 28 February 1999. Heavy solid line indicates floodplain inundation height of 21 400 ML day^{-1}. ▲ indicates sampling trip. Source: Theiss Environmental Services, Victoria.

and has a capacity of 40,000 ML (DWR 1989b). When Lake Nillahcootie is assured of filling, surplus water is released to Lake Mokoan, an off-stream storage. Lake Mokoan was constructed in 1971, by damming the Mokoan (or Winton) Swamp, and has a capacity of 365,000 ML (Harrison *et al.* 1990). Two diversion weirs, Casey's and Gowangardie, occur downstream of Benalla; both weirs are likely to be barriers to fish movement (Humphries and Lake 2000).

Despite these major storages, only about 10% of the river's mean annual discharge is diverted for offstream use. Flow regulation has resulted in increased summer to autumn flows and decreased winter to spring flows in the river (Cottingham *et al.* 2001a). The natural hydrology of the river is most severely altered in the section between Lake Nillahcootie and Benalla. The lower reaches of the river, downstream of Benalla, where the present studies occurred, have only been slightly affected by river regulation, and predominantly still retain the natural seasonal hydrological cycle, although the river now very rarely ceases to flow in summer (Humphries and Lake 2000, Cottingham *et al.* 2001a).

Water quality

Water quality is variable throughout the catchment, but generally good (Cottingham *et al.* 2001a). The lowland reaches of the river below Benalla, are rated as 'poor' in terms of total phosphorus and nitrogen concentrations, and have been assessed as in risk of blue-green algal blooms (GWQWG 1996). Other water quality issues in the catchment include increasing levels of salinity and turbidity, especially downstream of Casey's weir. Biocides (pesticides and herbicides) although frequently used in the catchment, have not been shown as yet to be a problem, however, it is of increasing public concern (GWQWG 1996).

The riverine environment

The riparian tree cover along banks of the river is fairly continuous (DWR 1989a). Between Lake Nillahcootie and Benalla, the riparian vegetation consists of a diverse range of native trees and introduced willows (*Salix spp.*). The riparian zone of the lowland reaches of the river consists of an open riverine grassy woodland, dominated by river red gum (*Eucalyptus camaldulensis*), scattered silver wattles (*Acacia dealbata*), black box (*Eucalypus largiflorens*) and exotic trees such as willows, with an understorey of sedges and grasses. While the majority of the red gum forests on the flood plain have been cleared for agricultural use, there are some extensive red gum forests still remaining along the river, which have been preserved either on private property or in riverside reserves.

The main channel in the lowland region of the river is ~ 30 m wide from bank to bank, with an extensive, periodically inundated flood plain (Figure 2.5). The flood plain contains numerous anabranches and billabongs (oxbow lakes). The river contains a diverse range of aquatic habitat types; including deep pools (up to 3 - 4 m), run sequences and still, shallow backwaters. There are also large numbers of snags (large woody debris) and patchy stands of emergent macrophytes, mostly *Phragmites australis*. Submerged macrophyte beds are less common, but where they do occur they are commonly either ribbon weed (*Vallisneria americana*) or water ribbon (*Triglochlin spp.*). Riverine substrate is largely dominated by sand, with only patchy areas of clay and bedrock substrates remaining. Large sand deposits due to erosion of the cleared catchment, are likely to have reduced the diversity of habitats available to fish, especially deep pool environments (Humphries and Lake 2000).

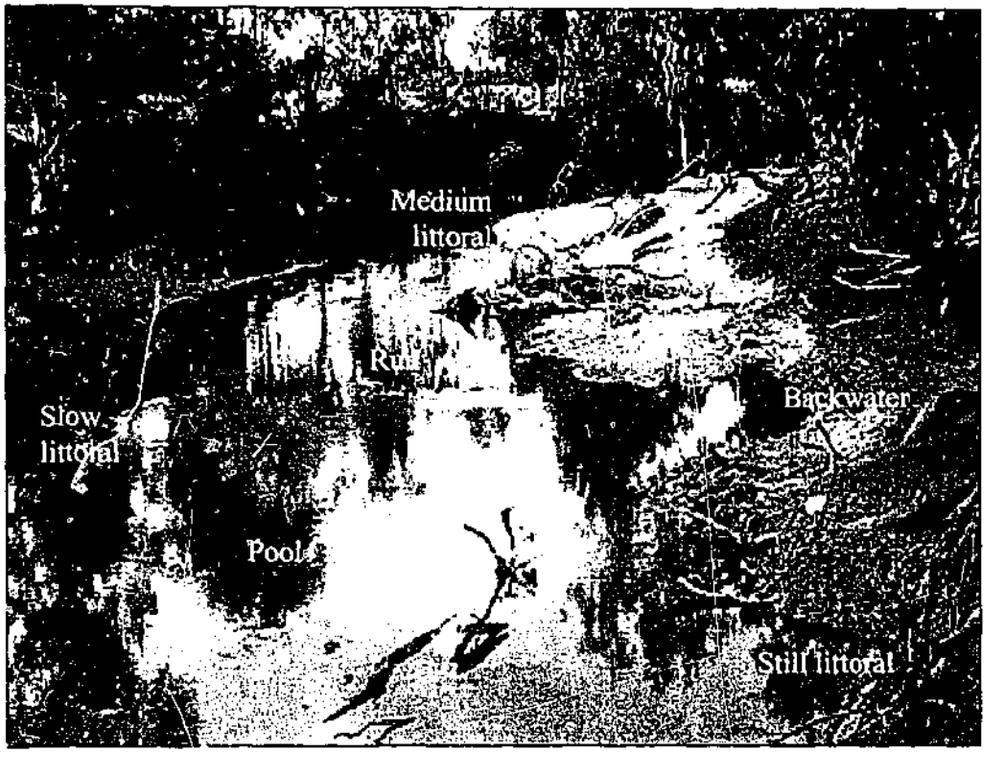


Figure 2.5: Broken River at the middle site. Labels indicate habitats sampled for larval fish (Chapter 4) and meiofauna (Chapter 6).

Fish community

The fish fauna in the Broken River downstream of Benalla is relatively diverse, with 13 native and four introduced fish species recorded (Table 2.2). Significant populations of a number of native species occur, including Murray cod, golden perch, Australian smelt, carp gudgeons and crimson-spotted rainbowfish (hereafter referred to as rainbowfish). Unfortunately, very little information exists about the historical distribution and abundance of native fish within the catchment, although anecdotally the river is reported to have contained significant Murray cod, silver perch, freshwater catfish (*Tandanus tandanus*) and river blackfish (*Gadopsis marmoratus*) populations. Of these four, only Murray cod and river blackfish remain in reasonable numbers today (P. Humphries, CRC for Freshwater Ecology, unpub. data). Four species that are known to exist in the Broken River are listed on the Victorian Flora and Fauna Guarantee Act, and two of these, silver perch and Macquarie perch, are threatened at a national level (Table 2.2). The most common introduced species are carp and *Gambusia holbrooki* (hereafter referred to as gambusia).

Recent studies in the river, have regularly found eight native and three introduced species occurring as larvae within the river (Table 2.2) (Humphries and Lake 2000, Humphries *et al.* in press). Composition of the larval fish fauna is dominated by Australian smelt, carp gudgeons, Murray cod and carp (Humphries and Lake 2000, Humphries *et al.* in press). Regular sampling of the larval fish community in recent years has suggested that the density of fish larvae is low compared with lowland rivers overseas (King and Humphries, unpub. data.).

Table 2.2: Fish species recently recorded in the Broken River downstream of Benalla and Ovens River downstream of Wangaratta and their conservation status. Source: Department of Natural Resources and Environment Victoria Fauna Atlas records post 1980 (T. Raadik, Department of Natural Resources and Environment, pers. comm.) and McDowall (1996). L = collected as larvae (Humphries and Lake 2000, Humphries *et al.* in press). Conservation status: FFG = listed as threatened under under the Flora and Fauna Guarantee Act, Victorian conservation status (shown in brackets) from DNRE (1999), National conservation status from ASFB (2001), CE = critically endangered, E = endangered, V = vulnerable, DD = Data deficient.

Common name	Scientific name (Authority)	Broken	Ovens	Conservation status	
				Victorian	National
Native species					
Australian smelt	*Retropinna semoni* (Weber)	* L	*		
Mountain galaxias	*Galaxias olidus* (Günther)	* L	*	(DD)	
Murray jollytail	*Galaxias rostratus* (Klunzinger)	*	+	(DD)	V
Crimson-spotted rainbowfish ‡	*Melanotaenia fluviatilis* (Castelnau)	* L	*	FFG (DD)	
Silver perch	*Bidyanus bidyanus* (Mitchell)	+	*	FFG (CE)	V
Golden perch	*Macquaria ambigua* (Richardson)	* L	*	(V)	
Macquarie perch	*Macquaria australasica* (Cuvier)	+	*	FFG (E)	V
Murray cod	*Maccullochella peelii peelii* (Mitchell)	* L	*	FFG (V)	
Trout cod	*Maccullochella macquariensis* (Cuvier)		*	FFG (CE)	E
River blackfish	*Gadopsis marmoratus* (Richardson)	+	*		
Western carp gudgeon †	*Hypseleotris klunzingeri* (Ogilby)	* L	*		
Lake's carp gudgeon †	*Hypseleotris sp. 5* (Undescribed)	* L	*		
Midgley's carp gudgeon †	*Hypseleotris sp. 4* (Undescribed)	* L	*		
Flathead gudgeon	*Philypnodon grandiceps* (Krefft)	*	+		
Southern pygmy perch	*Nannoperca australis* (Günther)		*		
Flyspecked hardyhead	*Craterocephalus stercusmuscarum fulvus* (Ivantsoff, Crowley and Allen)		*	FFG (DD)	
Introduced species					
Carp	*Cyprinus carpio* (Linnaeus)	* L	*		
Goldfish	*Carassius auratus* (Linnaeus)	*	*		
Redfin perch	*Perca fluviatilis* (Linnaeus)	* L	*		
Gambusia #	*Gambusia holbrooki* (Girard)	* L	*		
Oriental weatherloach	*Misgurnus anguillicaudatus* (Cantor)		*		

† = The taxonomy of carp gudgeons is uncertain due to the presence of hybrids (Bertozzi *et al.* 2000). In general, the three species of carp gudgeons known to occur in the Ovens and Broken Rivers are referred to as a species complex of carp gudgeons hereafter. The exception is in chapter 3 where species richness measures were important in the analysis.

= *Gambusia holbrooki* is commonly referred to as Mosquitofish as a common name, however, hereafter the common name used for this species will be gambusia, following the convention of McDowall (1996).

‡ = Crimson-spotted rainbowfish, hereafter referred to as rainbowfish.

2.3 The Ovens River

The Ovens River catchment which covers an area of approximately 780,000 ha (Figure 2.6), rises in the Great Dividing Range in the Alpine National Park and flows 150 km north where it joins the Murray River at Lake Mulwala; a diversion weir. The river has two major tributaries, the Buffalo and King Rivers, which join the Ovens River near the towns of Myrtleford and Wangaratta respectively (Figure 2.6). The valley widens downstream of Wangaratta, with inputs from Reedy and Fifteen Mile Creeks, and then flows across the riverine flood plain and into Lake Mulwala. The Ovens River system is one of the least regulated rivers in the southern region of the Murray-Darling Basin (Cottingham *et al.* 2001b).

The present study was conducted in the lower reaches of the river downstream of Wangaratta, at the Peechelba bridge crossing, in Lavis Bend State Forest (Figure 2.6 & 2.7). Sampling was conducted on the flood plain during both high and low flow periods, in the spring and summer of 1998, 1999 and 2000.

Brief history and land use

In 1824, the explorers Hamilton Hume and William Hovell crossed the lower Ovens River, and named it after the Irish-born soldier, Major John Ovens, who was aide-de-camp to the Governor of Brisbane at the time (DNR 1989b). By the late 1830's the lower Ovens area was settled by squatters, who grazed cattle and sheep. The population of the region rapidly increased following the discovery of gold in the Beechworth area in 1852. Most of the present day agricultural land was cleared by the late 19th century (DNRE 1998). The natural geomorphic features of the river have been altered by gold mining in the upper reaches, intensive floodplain clearing and cultivation, and river 'improvement' works such as desnagging, willow planting and channel stabilisation (Cottingham *et al.* 2001b). The lower reaches of the river, where the present study was conducted, have been disturbed little by desnagging or other river 'improvement' works, and therefore this reach retains a close-to-natural flood regime (Cottingham *et al.* 2001b).

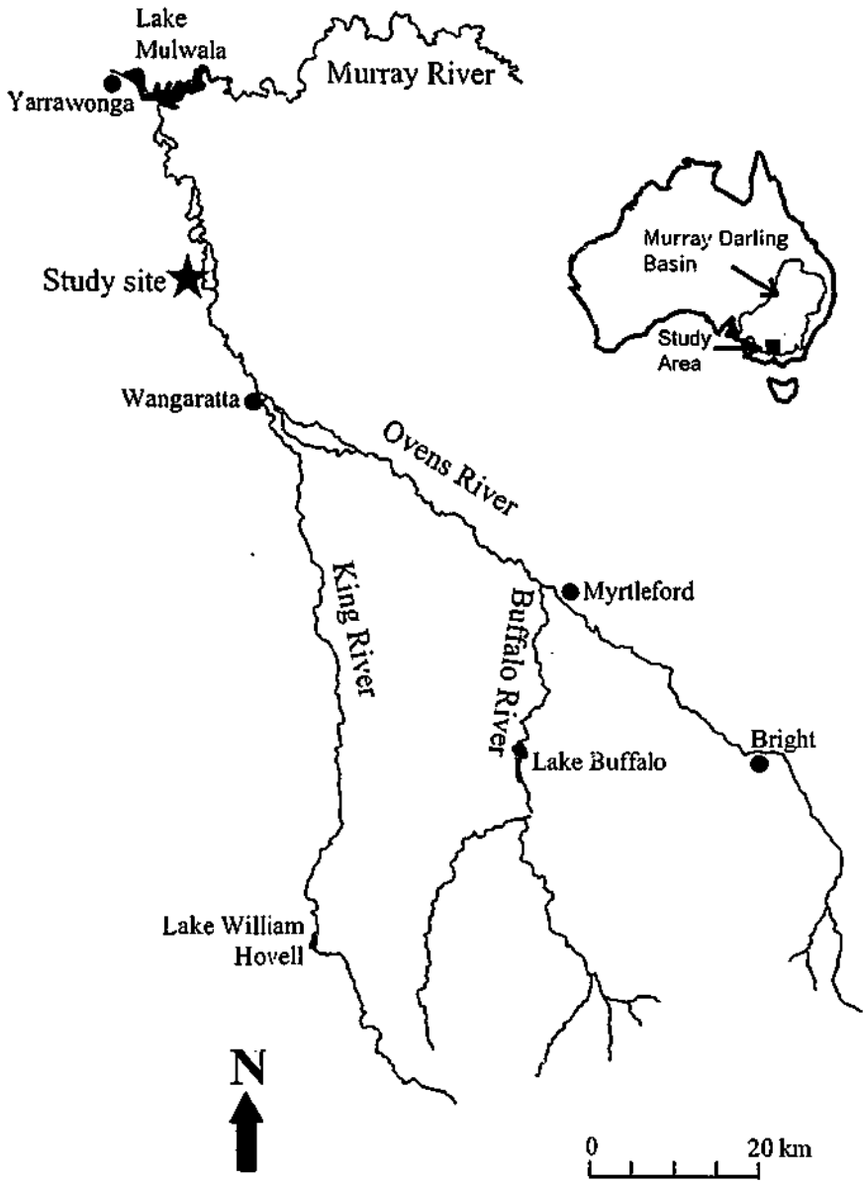


Figure 2.6: Map of Ovens River catchment.

(a)

(b)

Figure 2.7: (a) Ovens River downstream of Peechelba bridge (Photo courtesy of B. Gawne, Murray-Darling Freshwater Research Centre) and (b) flood plain during flood conditions in October 2000.

The major land use in the Ovens River catchment is public land (Table 2.3), consisting of mainly forested and mountainous regions, which are reserved as either National Park or State Forest. Dryland grazing of beef cattle and sheep, pine plantations, and broadacre cropping occur in the lower catchment. The more fertile land along the Ovens and King River valleys is used for intensive horticulture and dairying. Traditionally, tobacco and hops were grown in the valleys; however, increasingly these farms are diversifying into new crops such as vegetables and wine grapes (DNRE 1998). The population of the catchment is approximately 45,000, of which 35% live in Wangaratta.

Table 2.3: Major land use types in the Ovens River catchment. Source: DNRE (1998).

Land use	Area (ha)	% of total
Broadacre grazing and cropping	92990	12.0
Dryland grazing	232870	30.2
Irrigated grazing	1130	0.1
Horticulture – annuals and perennials	7290	0.9
Pine plantations	27030	3.5
Remnant native vegetation (private land)	36340	4.7
Public land (mostly National Park and State Forest)	368190	47.7
Urban area	2815	0.4
Water bodies	3200	0.4
Total	**771855**	

Geomorphological character

The Ovens River flows through four major geomorphic zones (Cottingham *et al.* 2001b):

Zone 1: Headwater zone: Hilly to mountainous terrain on lower Palaeozoic sedimentary rocks in the upper catchments. The River floor is dominated by bedrock.

Zone 2: Confined valley zone: Confined flood plains and terraces downstream of the mountain front, extending to Moyhu on the King River, and Markwood on the Ovens River. The active flood plain of the river in this reach varies from 500 m to about 3 km in width. This zone of the river is characterised by a gravel bed, with well-defined pool-riffle morphology, and rapid rates of bank erosion and floodplain scouring.

Zone 3: Upper anabranching reach: The flood plain widens dramatically at this point, and the bed material becomes finer. There a rapid transition in the main channel of

the Ovens River from a gravel bed, pool-riffle stream at Tarrawingee, to a sandy, anabranching stream at the King River confluence. This important transition marks a decrease in stream and valley slope, and the beginning of an anabranching system of channels.

Zone 4: Lower confined reach: Downstream of the Ovens and King River junction, the river enters the Riverine Plains proper. Importantly, the flood plain of the river becomes more confined downstream as the river incises into the Shepparton Formation of the Riverine Plains. The river below the Reedy Creek Junction is sinuous, with clay banks, and a sandy to fine gravel bed. The channel maintains permanent flow, and frequent flooding. The flood plain is made up of wetlands created by meander cutoffs.

Climate

Climate varies considerably with topography and elevation within the Ovens River catchment. Mean annual rainfall ranges from 2,000 mm in the upper alpine areas to around 500 mm on the plains near Yarrawonga. Winter snowfalls are common above 1000 m, with much of the high ground generally covered in snow between June and October.

Wangaratta, the nearest regional centre to the site used in this study, experiences a similar climate to Benalla, with cool wet winters (mean daily minimums and maximums, 3.1 - 14.6 °C) and hot dry summers (13.3 - 31.0 °C) (Figure 2.8a) (Bureau of Meteorology). Mean annual rainfall is approximately 637 mm, with maximum falls from June to August and minimum falls from December to February (Figure 2.8b) (Bureau of Meteorology).

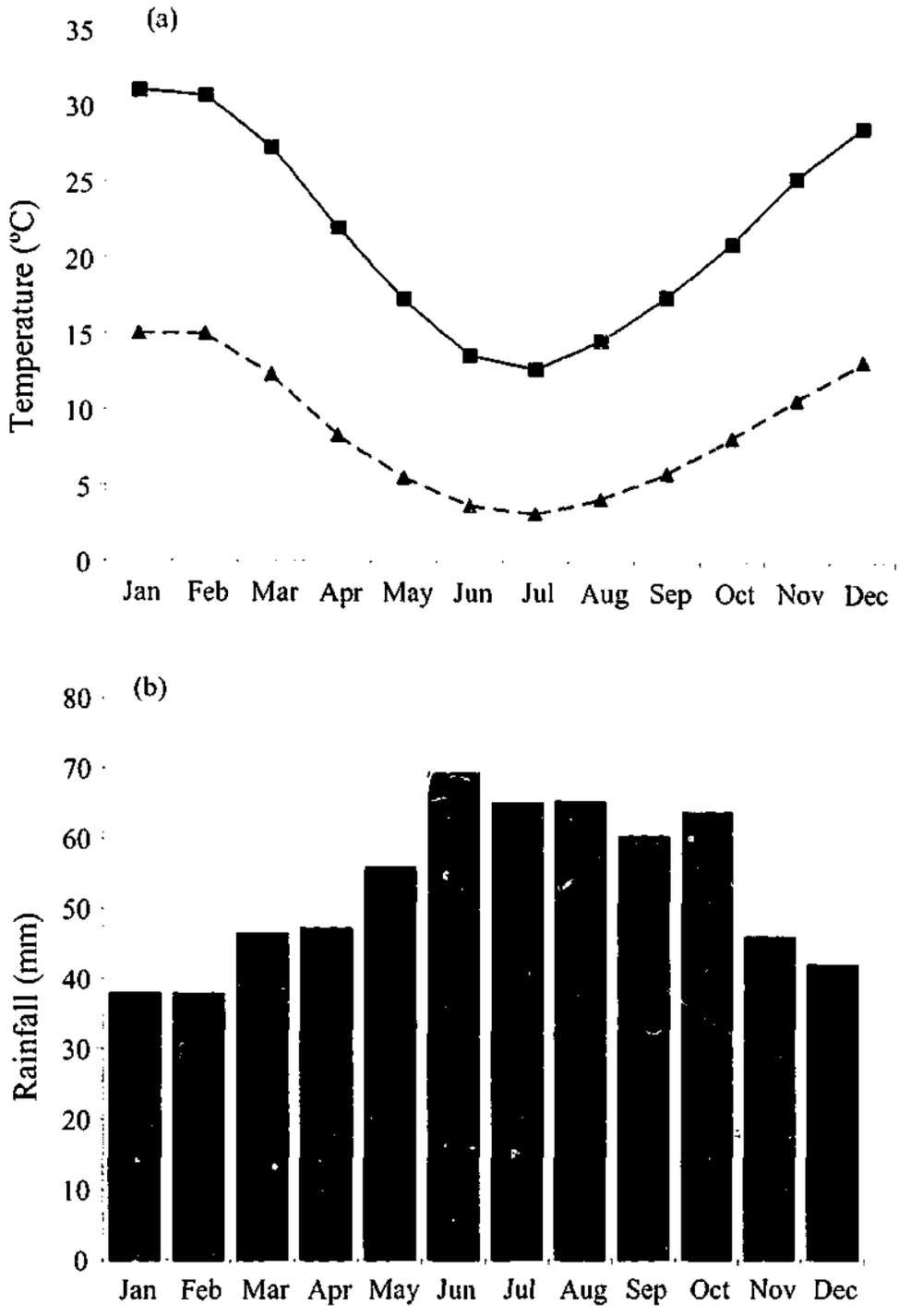


Figure 2.8: (a) Monthly mean maximum (—■—) and minimum (--▲--) air temperatures and (b) monthly mean rainfall at Wangaratta. Source: Bureau of Meteorology.

Hydrology and water storages

The Ovens River remains one of the least regulated lowland rivers in the Murray-Darling Basin. Flooding occurs seasonally during winter and spring in most years, triggered by a combination of heavy rainfall and snowmelt. The mean annual discharge of the Ovens River is 1,620,000 ML (DWR 1989b). Only two small storages are present in the catchment, Lake Buffalo on the Buffalo River (24,000 ML) and Lake William Hovell on the King River (13,500 ML) (DNRE 1998). These storages are located in the forested mountain slopes of the upper catchment. Some extraction of water for agricultural use does occur, but is only ~ 1.5% of the total annual discharge.

From previous studies conducted on the river and personal observations during winter and spring 1998, the billabongs sampled during the study at Peechelba are connected to the main channel at approximately 15,000 ML day^{-1} (pers. obs., T. Hillman, CRC for Freshwater Ecology, pers. comm.). Significant flooding occurred during the period of the study described in chapter 7, especially in 1998 and 2000 (Figure 2.9).

Water quality

The water quality conditions throughout the Ovens catchment are considered to be good (Cottingham *et al.* 2001b). Water quality varies throughout the catchment and with flood and rainfall events, and generally decreases in quality downstream (Cottingham *et al.* 2001b). The lowland region of the river has been rated as poor to moderate, in terms of total phosphorus and nitrogen concentrations (DNRE 1998). Turbidity and salinity are generally low, but tend to increase downstream (DNRE 1998). Significant levels of pesticide residues have been detected in both sediments and aquatic organisms along the river; however, the levels are generally quite low and are not considered to be a major threat (DNRE 1998).

The floodplain environment

Although modified by human activities and the introduction of weed species, the lowland reaches of the river still retain extensive river red gum (*Eucalyptus camaldulensis*) forests on the flood plains downstream of Wangaratta (Cottingham *et al.* 2001b). The 1-2 km wide corridor on either side of the river has been preserved mainly as State Forest. Lavis Bend State Forest is an open river red gum forest, which has been logged in the past and is still used for cattle grazing under lease arrangement. The understorey is mainly dominated

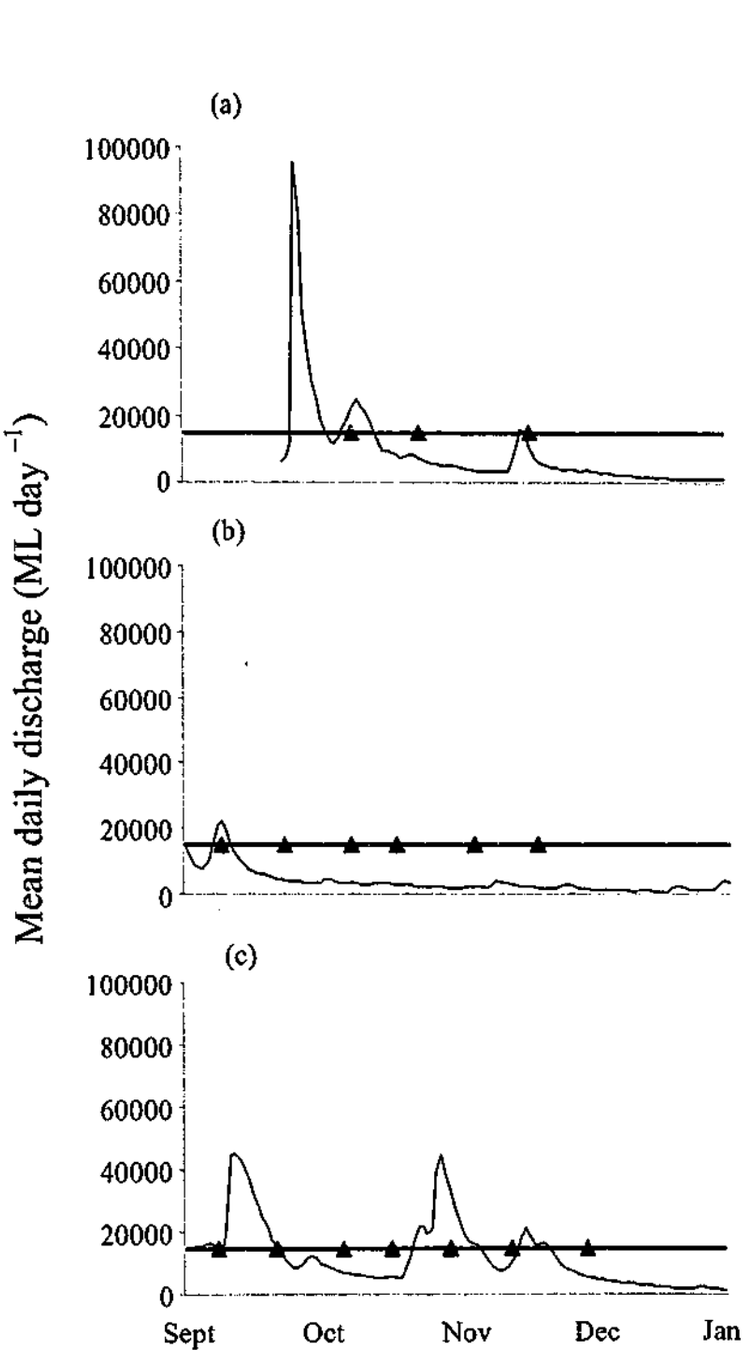


Figure 2.9: Mean daily discharge (ML day^{-1}) (thin solid line) for the Ovens River at Peechelba between (a) 22 September to 31 December 1998, (b) 1 September to 31 December 1999, and (c) 1 September to 31 December 2000. Heavy solid line indicates flood plain inundation height (15,000 ML day^{-1}), ▲ indicates sampling trip. Note: Flow data were unavailable for 1 – 22 September 1998 due to gauge malfunction. Source: Theiss Environmental Services, Victoria.

by a dense scrub of wattles (*Acacia* sp.), tea-tree (*Leptospermum* sp.) and bottlebrushes *Callistemon* sp.). The perennial native grass and herb communities still remain, with some exotic species present (Cottingham *et al.* 2001b) (Figure 2.7a & b).

A large number of permanent and temporary billabongs are present on the flood plain, and vary in morphology, size, depth and vegetation cover. The presence and abundance of macrophytes in the billabongs varies throughout the year and in response to the water regime. In a study of the ecology of crayfish in billabongs of the Ovens River flood plain, 14 macrophyte taxa were recorded from eight billabongs (Brooks 1997). During the wet phase, the most common macrophyte taxa present in the billabongs are *Triglochin multifructum, Myriophyllum papillosum, Stellaria angustifolia, Pseudoraphis spinescens, Potamogeton tricarinatus* and *Eleocharis acuta* (Brooks 1997, Quinn *et al.* 2000).

Fish community

Sixteen native and five introduced fish species have been recorded from the Ovens River downstream of Wangaratta (Table 2.2). The river supports a healthy and diverse native fish community, with recreationally important species such as Murray cod and golden perch abundant in the lowland reaches, and large populations of small native species such as Australian smelt and carp gudgeons (J. Koehn and T. Raadik, Victorian Department of Natural Resources and Environment, pers. comm.). The fish community of the lowland reaches of the river is of high conservation significance, with six species listed on the Victorian Flora and Fauna Guarantee Act and four of these listed as nationally threatened or rare (Table 2.2). Very little information exists about the historical distribution and abundance of native fish within the catchment, although the river is anecdotally reported to have contained significant populations of Macquarie perch (*Macquaria australasica*), silver perch and freshwater catfish. Five introduced fish species occur in the river. Carp, goldfish (*Carassius auratus*), redfin perch (*Perca fluviatilis*) and gambusia are in significant numbers throughout the catchment. Oriental weatherloach (*Misgurnus anguillicaudatus*) were first recorded within the catchment in a small tributary in 1985, but have rapidly spread downstream to the Murray River (T. Raadik, pers. comm.). The present abundance and status of this species in the catchment is not known.

The fish community differs substantially between the main river channel and the billabongs on the adjacent flood plain (Table 2.4). Large native species are rarely recorded

in billabong habitats, with introduced species and small native more common. The composition of the fish communities in billabongs varies greatly, even between adjacent billabongs (G. Closs, University of Otago, pers. comm. and D. McNeil, LaTrobe University, pers. comm.). To date there have been no published studies on the fish communities in the Ovens River.

Table 2.4: Fish species in the Ovens River and their occurrence in river and billabong habitats. Source: McDowall (1996) and Department of Natural Resources and Environment Victoria Fauna Atlas, records post 1980 (T. Raadik, Department of Natural Resources and Environment, pers. comm.).

Common name	River	Billabong
Native species		
Australian smelt	*	*
Mountain galaxias	*	
Murray jollytail		*
Golden perch	*	
Murray cod	*	
Macquarie perch	*	
River blackfish	*	
Western carp gudgeon	*	*
Lake's carp gudgeon	*	*
Midgeley's carp gudgeon	*	*
Flathead gudgeon	*	
Southern pygmy perch		*
Flyspecked hardyhead		*
Introduced species		
Carp	*	*
Goldfish	*	*
Redfin perch	*	*
Gambusia	*	*
Oriental weatherloach		*

Chapter 3: Description and Evaluation of a New Method for the Collection of Small Fish - The Sweep Net Electrofishing (SNE) Method

3.1 Introduction

There is a diversity of gear types currently available for the collection of larval and juvenile fish in freshwater habitats. Commonly used techniques include light traps, baited traps, drift and trawl nets, electrofishing, pump samplers, sweep nets and seine nets (for review see Kelso and Rutherford 1996). These collection techniques have been developed because of the need to sample a range of species with diverse behaviours, reproductive strategies and habitat preferences. However, a major limitation is that no single technique is equally effective for all species, nor over the entire range of early development for a particular species. To enable rigorous comparisons of ontogenetic changes within a species, particularly studies of microhabitat use, it is an advantage to use one standardised collection method that samples effectively throughout the various stages of early development (Copp 1989a, Copp and Garner 1995).

A commonly used technique for the collection of freshwater fish is electrofishing, where pulsed electricity is used to immobilise individuals so that they can be collected using hand or sweep nets (see Kelso and Rutherford 1996). However, size selectivity using electrofishing techniques has been commonly described, with larger fish usually more vulnerable to capture than small fish (Reynolds 1996). Electrofishing for small fish, particularly larvae, has been generally regarded as ineffective and is not widely used (Copp 1989a, Kelso and Rutherford 1996). However, Copp and Penaz (1988), Copp (1989a) and Copp and Garner (1995) described simple modifications that can be made to a standard backpack electrofishing unit to increase the capture of larval and juvenile fish. By reducing the diameter of the anode to 10 cm, and thereby increasing the voltage gradient surrounding the anode, they were able to collect large numbers of larval and juvenile fish. The procedure used in these studies usually involved a standardised sampling strategy, termed point abundance sampling (Nelva *et al.* 1979), where a large number of small point samples were collected to characterise patterns at the study site. This sampling strategy has been used in a number of studies that have attempted to assess quantitatively microhabitat use by larval and juvenile fish (eg. Copp and Penaz 1988, Copp 1992 a & b, Garner 1996, Watkins *et al.* 1997, Gozlan *et al.* 1998, Jurajda 1999).

Despite its widespread use, there has been relatively little study of the efficiency of the point abundance electrofishing (PAE) method for the collection of fish (although see Garner 1997). Garner (1997) compared the densities and standard lengths of fish collected using the PAE with those collected using a standard seine net, and concluded that there was little difference between the length-frequency distributions of fish collected by the two methods. However, he suggested that density data from PAE studies should be treated with caution, owing to the large amount of variation between samples. In common with other electrofishing methods, the effectiveness of the PAE method may also vary with current speed, water conductivity (Hill and Willis 1994), habitat complexity, depth (Reynolds 1996), voltage, direction of movement of target individuals within the electric field and water temperature (Regis *et al.* 1981).

This chapter describes a simple modification to a standard backpack electrofishing unit that allows for the effective and habitat-specific collection of small bodied fish. The sweep net electrofishing method is compared with two commonly used methods, a sweep net and the point abundance electrofishing method described by Copp and Penaz (1988). For each of the three methods, the numbers of individuals, species richness and length-frequencies of fish collected from habitats differing in water velocity were examined.

3.2 Materials and Methods

Description of the sweep net electrofishing method

A portable backpack electrofisher (Smith-Root Model 12), with standard braided wire cathode and 15 cm diameter anode, was modified by attaching a moulded plastic (High Density Poly Ethylene [HDPE]) rectangular frame (25 x 30 x 2 cm) to the bottom of the anode pole (Figure 3.1). The frame was attached by pushing the bottom portion of the two piece anode pole through a hole at the top of the frame, until the anode ring was in the middle of the frame and then firmly tightened using an HDPE formed screw. The frame was easily fitted to a standard anode pole without any alteration to the electrofishing unit itself. As the frame was manufactured from non-conductive HDPE, minimal disturbance was caused to the electrical field surrounding the anode. A removable 250 µm mesh net was fastened to the frame using Velcro™ attachments (Figure 3.1). The net tapered to a removable collection jar (8.5 cm diameter).

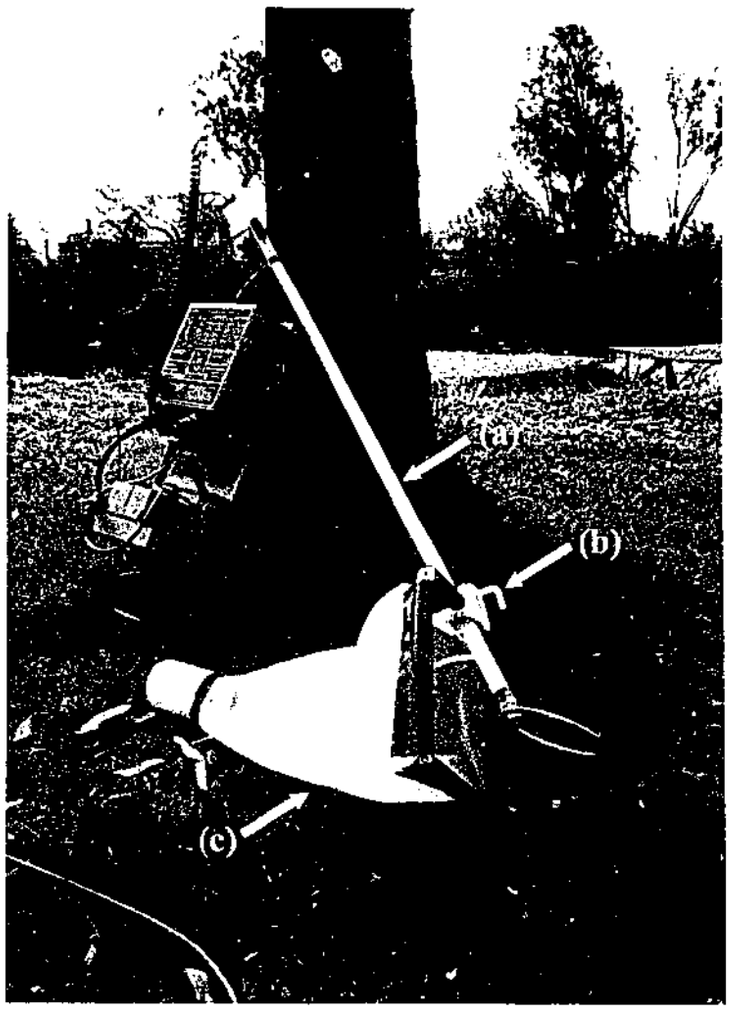


Figure 3.1: Modifications made to a standard backpack electrofishing unit for the SNE method. (a) Anode pole with attached 15 cm diameter anode, (b) plastic formed screw and frame, (c) Nylon material with velcro lining for attaching 250 µm mesh net to plastic frame.

Whilst this equipment has the potential to be used in a number of different ways, depending on the objectives of the study, the method was developed principally to sample fish from specific habitats within the flood plain and the main channel of rivers (King, unpub. data and Chapters 4 and 7). The sampling protocol involved approaching selected habitats quietly; in rivers this was always from a downstream direction. The activated anode, with attached frame and net, was moved at a constant speed in a forward zig-zag motion to cover all the available depths of the habitat, similar to the use of a normal sweep net. Sampling was divided into 2 x 10 second periods, allowing the operator to move to a different position between periods within the designated habitat, thus reducing the potential problem of herding fish away from the collection net. Electrofishing was conducted by one operator, with another person always present for sample preservation and safety reasons.

Study period

A comparison of the three methods was conducted over three days (11 November, 21 and 22 December 1999) at a different site each day, on the Broken River in north-eastern Victoria, Australia. The three sites used in the study were in the lowland region of the river. For a description of the river see section 2.2. During the study period, water temperature ranged from 19.0 to 26.1 °C, dissolved oxygen from 4.8 to 10.7 mg L^{-1}, pH from 7.0 to 8.2, conductivity from 153 to 257 µS cm^{-1}, and turbidity from 63 to 150 NTU. Water quality variables were measured using a Horiba Water Quality Checker (Horiba Ltd, Japan) at three randomly selected sampling points at each site.

Comparison of methods

The efficacy of the sweep net electrofishing method (SNE) was compared with two other methods: a standard sweep net (SW) and the point abundance electrofishing method (PAE) described by Copp and Penaz (1988). These methods were chosen for comparison because they are both active methods and are commonly used to capture small fish (Kelso and Rutherford 1996). The SNE method was used to sample each habitat replicate as described above. For the SW method, a net with a 28 x 30 cm opening and 250 µm mesh was used. This net was swept through each sampled habitat replicate at a constant speed in a zig-zag motion, with sampling divided into 2 x 10 second periods, thereby covering the same area as the SNE method. For the PAE method, one operator with the backpack electrofisher

immersed the 15 cm anode ring to half the water column depth and activated the anode for 5 seconds. A second operator then swept a 250 µm mesh sweep net (28 x 30 cm) through the sampling point to collect immobilised fish and shrimp. The PAE method is usually used at randomly allocated points to collect a large number of small-sized samples within a site (Copp 1989a). To ensure that a similar area was sampled by each method, five PAE samples were taken in each habitat and these samples were pooled to represent one habitat replicate.

The effectiveness of the methods under different current speeds was determined by sampling three current speed categories (still, slow and medium). Water velocity in each habitat was determined by placing the sweep net in the water and observing any ballooning of the net. If no movement of the net occurred, the habitat was considered 'still', slow ballooning of the net indicated a 'slow' habitat, and rapid ballooning indicated a 'medium' habitat (Copp 1992b). This water velocity estimation technique was evaluated using a current meter (Hydrological Services, Model No. CMC-200), where three measurements of water velocity were taken within six replicate habitats of each velocity category. Still habitats ranged in speed from 0 to 0.02 m s^{-1} (mean ± SE = 0.02 ± 0.00), slow habitats from 0.07 to 0.22 m s^{-1} (0.16 ± 0.04) and medium habitats from 0.17 to 0.47 m s^{-1} (0.32 ± 0.04). Areas with high current speeds were not sampled in this study, due to the difficulty of sampling with the three methods in fast flowing water, and because larvae are rarely found in fast flowing habitats (Lightfoot and Jones 1996, see also Chapter 4).

To maximise the number of larval and juvenile fish collected, sampling in this study was restricted to littoral areas. All habitats were < 75 cm in depth, with sandy clay substrates and varied in the amount of woody debris and macrophyte cover. At each site, 15 replicates of each water velocity category were selected, until five samples for each method had been collected. All habitats were sampled during daylight hours.

Samples were collected in the attached removable collection jar, and the whole sample was preserved in 95% ethanol. All fish were removed from the samples and identified in the laboratory under a dissecting microscope. Identifications were made using published and unpublished descriptions and keys (Lake 1967b, McDowall 1996, Neira *et al.* 1998, Humphries, unpub., see Appendix A). The taxonomy of carp gudgeons is uncertain due to the presence of hybrids (Bertozzi *et al.* 2000), however, for the purposes of this study,

where species richness was important, adult carp gudgeons were identified to one of the three species as described in Larson and Hoese (1996). The standard lengths of all fish < 10 mm were measured using an eyepiece graticule, and fish > 10 mm were measured using vernier callipers, all to 0.1 mm.

Data analysis

As estimates of density based on electrofishing samples may be seriously biased (Reynolds 1996), and because the efficiencies of the three methods have not been comprehensively assessed, the data was treated as catch per unit effort, rather than an absolute density estimate. Due to the low numbers of fish caught at each site, data were pooled across the three sites in the analysis. Two-way analysis of variance (ANOVA) with 'method' and 'velocity category' as fixed factors (df = 2 for both factors), was used to examine differences in species richness and total number of fish. Data for the total number of individuals (larvae, juveniles and adults) and total number of larvae were $\log_{10}$ (x+1) transformed to meet the normality and homogeneity of variance assumptions of ANOVA. Species richness data did not require transformation, and included where applicable the three species of carp gudgeons when identified as adults. *Post hoc* analysis was carried out on significant factors using Tukey's test. Kolmogorov-Smirnov tests were used to assess whether the frequency distributions of fish lengths differed among the three methods. Statistical analyses were carried out using SYSTAT ™ (Wilkinson 1990) software, and significance levels for all analyses were set at $P < 0.05$.

3.3 Results

A total of 210 fish from eight species were collected during the study (Table 3.1). Of this total, 160 larvae from four species were collected; Australian smelt, rainbowfish, carp and gambusia. Lake's carp gudgeon, Midgeley's carp gudgeon, western carp gudgeon and redfin perch were collected only as juveniles or adults.

Table 3.1: Total number of individuals, total number of larvae and average number of individuals of fish per sample (1 SE) collected using sweep net electrofishing (SNE) method, sweep net (SW) method and the point abundance electrofishing (PAE) method. n = number of replicate samples.

Method	n	Total individuals	Total larvae	Average number per sample
SNE	45	126	100	2.80 (1.05)
SW	45	63	52	1.40 (0.48)
PAE	45	21	8	0.47 (0.17)

The total number of individuals and the number of larvae varied significantly by 'method' and 'velocity category', with no significant interaction between the two factors (Table 3.2). The SNE method captured a higher number of total individuals and larvae than both the SW and PAE methods (Table 3.1). However, due to large inter-sample variation, there was no significant difference between the total number of individuals ($P > 0.05$) or the number of larvae (Figure 3.2a & b, $P > 0.05$) captured per sample using the SNE method and the SW method. By contrast, there was a significantly greater number of total individuals (Figure 3.2a, $P < 0.01$) and larvae (Figure 3.2b, $P < 0.001$) captured in the SNE method than the PAE method. There was no significant difference between the catches of total individuals in the SW method and the PAE method (Figure 3.2a, $P > 0.05$), although significantly more fish larvae were collected in the SW method compared with the PAE method (Table 3.1, Figure 3.2b, $P < 0.05$). Both the total number of individuals and the number of larvae was greater in still habitats than slow ($P < 0.001$) and medium flowing habitats ($P < 0.001$), whereas there was no significant difference between catches in slow and medium flowing habitats (Figure 3.2a & b, $P > 0.05$).

Table 3.2: Mean squares and significance levels for results of 2-way analysis of variance on total individuals, number of larvae and number of species, with 'method' and 'velocity category' as factors. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Factor	df	Total individuals	Number of larvae	Number of species
Method	2	0.457 **	0.512 **	2.696 ***
Velocity	2	2.266 ***	1.288 ***	12.652 ***
Method x Velocity	4	0.113	0.131	0.774 *
Error	126	0.074	0.065	0.315

The number of species collected differed significantly among 'method' and 'velocity category' (Table 3.2). A significant interaction also occurred between 'method' and 'velocity category', but explained little of the overall variance (Table 3.2). There were consistently more species collected in the still habitats compared with the slow (P < 0.001) and medium flowing habitats (P < 0.001), irrespective of the method used for collection (Figure 3.2c). There was no significant difference between the number of species collected per sample in slow and medium flowing habitats (Figure 3.2c, P > 0.05). The SNE method collected significantly more species per sample than the PAE method (Figure 3.2c, P < 0.001), while the number of species collected in the SW method did not differ significantly from the other two methods (Figure 3.2c, both methods P > 0.05).

The length-frequency distributions of catches of fish between the three methods were significantly different (Figure 3.3a, Table 3.3). All methods caught a similar minimum size (Table 3.3). However, only 24 % of fish collected using the PAE method were below 10 mm in length, compared with 60 % and 74 % of the catches in the SNE and SW methods, respectively (Figure 3.3a). The maximum size was restricted to less than 20 mm in the SW method, whereas 16 % and 29 % of the catches using the SNE method and the PAE method, respectively, were greater than 20 mm in length (Figure 3.3a).

Table 3.3: Differences between size range, mean and median lengths, and the length-frequency distributions of fish using Kolmogorov-Smirnov (J) tests of the three methods. SNE = Sweep net electrofishing method, SW = Sweep net method, PAE = point abundance electrofishing method. ** = P < 0.01, *** = P < 0.001.

Method	Range (mm)	Mean (1 SE)	Median	J		
				SNE	SW	PAE
SNE	4.5 – 42.6	11.62 (0.63)	9.5	-		
SW	4.4 – 19.1	8.34 (0.39)	7.5	**	-	
PAE	4.0 – 61.9	17.54 (2.54)	16.2	***	***	-

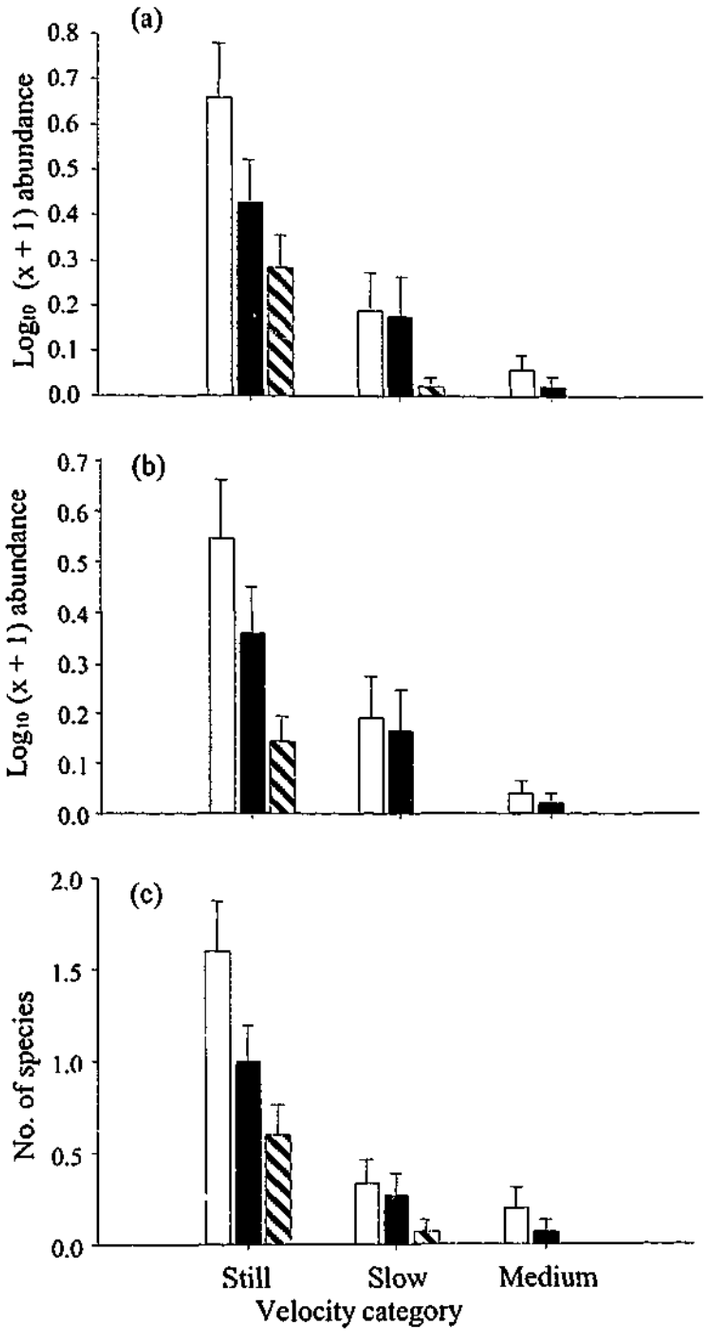


Figure 3.2: Mean (+1 SE) number of (a) total individuals, (b) larval fish and (c) species by method and velocity category. SNE method (open bars), SW method (closed bars), PAE method (striped bars). Note different y-axis scales.

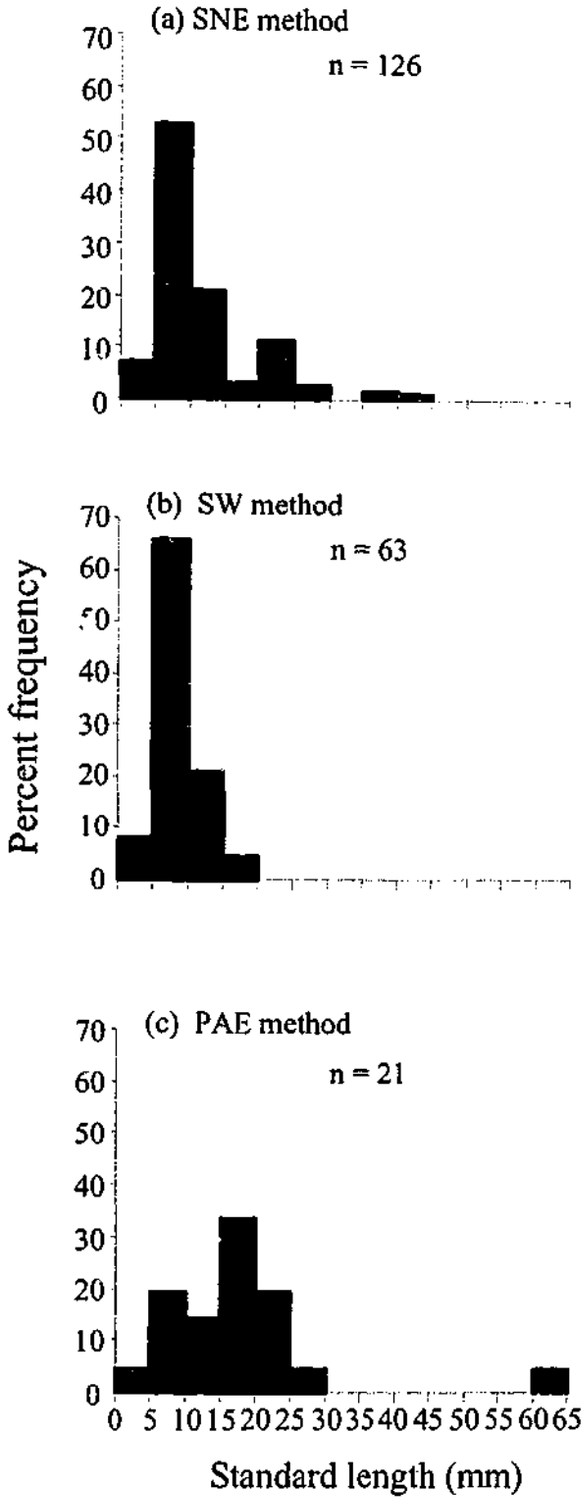


Figure 3.3: Length-frequency distributions as percentage of each size class (5 mm intervals) of fish for (a) SNE (sweep net electrofishing) method, (b) SW (sweep net) method and (c) PAE (point abundance electrofishing) method.

3.4 Discussion

The three methods evaluated in this study differed in their efficacy in collecting small fish. The SNE method collected more individuals than the other two methods and a greater size range than the SW method. The size ranges of fish captured by the two electrofishing methods were similar, although the SNE method collected a larger proportion of small fish larvae than the PAE method. The upper size limit of fish captured in the SW method was lower than that of the two electrofishing methods. It is likely that larger fish were able to escape the SW method, since larger fish have better swimming capabilities than smaller fish (Meng 1993, Lightfoot and Jones 1996). Larger fish were captured more effectively where electricity was used, as they are generally more vulnerable to capture than small fish using electric fields (Reynolds 1996). Consequently, the SW method appears to provide samples of fish that are skewed towards smaller size classes compared with the two electrofishing methods.

Water velocity had a significant effect on the number of fish collected by each of the three methods, with the greatest numbers collected in still habitats and the least in medium flowing habitats. The low number of fish collected in flowing habitats is likely to reflect habitat utilisation patterns of the larval and juvenile fish (Schiemer *et al.* 1991, Lightfoot and Jones 1996, Wintersberger 1996, see Chapter 4), rather than an inability of the three methods to collect fish in flowing water. Catches of fish were so low in flowing habitats, that it is difficult to assess how the methods compared with each other under these conditions. However, the PAE method caught significantly fewer fish in medium and slow flowing habitats than the other two methods. This may be because individuals shocked with the PAE method have the potential to drift away with the flow before capture (Copp and Garner 1995, Garner 1997). An advantage of the SNE method over the PAE method in flowing environments is its ability to immobilise fish and immediately capture them in the net fixed to the anode pole. Similarly, the SW method does not permit fish to drift downstream, although it seems to allow larger fish to actively avoid capture. However, all three methods are difficult to use in faster flowing waters (> 0.5 m s^{-1}), and sampling in these velocities is therefore usually restricted to passive drift netting.

Assessment of the abilities of the three methods to capture the range of species present is limited due to the study's restricted temporal scale, which limits the number of species present as larvae, and the low species diversity characteristic of temperate Australian

lowland rivers (McDowall 1996). In longer-term studies of more diverse fish assemblages, much larger numbers of fish species were collected using the PAE method (Copp and Penaz 1988, Copp 1992a & b, Garner 1996, Watkins *et al.* 1997, Gozlan *et al.* 1998, Jurajda 1999). In a longer-term study using the SNE method, 80 % of species known to occur in the Broken River were collected (see Chapter 4). The longer-term study, combined with the results of the present study, suggests that the SNE method is capable of collecting as wide a range of species as the PAE method.

In this study, the PAE method captured fewer fish than both the SNE and SW methods. However, a number of studies have successfully used the PAE method to capture large numbers of small fish (Copp and Penaz 1988, Copp 1992a & b, Copp *et al.* 1994, Garner 1996, Gozlan *et al.* 1998, Jurajda 1999). One possible explanation for the difference is the high density of fish found in these European river systems compared with the Broken River and other similar lowland rivers in south-eastern Australia (Humphries *et al.* in press, King and Humphries, unpub. data). In rivers where the density of fish larvae is low, the sampling method must be able to capture the maximum number of fish possible across all habitat types present, to enable rigorous statistical analysis.

Brosse *et al.* (1999) compared the PAE method with point abundance sampling based upon visual counts, in a microhabitat study of fish in the littoral zone of a European reservoir. Although they found that the estimated occurrence and abundance of the target species (roach, *Rutilus rutilus*) was similar between the two methods, they found serious discrepancies in estimates of microhabitat use between the methods. Brosse *et al.* (1999) suggested that the PAE method biased the estimated microhabitat use of 0+ roach by inducing an escapement behaviour in the fish, causing them to shelter in shallow water amongst dense vegetation. In common with most other active collection techniques (Hayes *et al.* 1996), the SNE method also has the potential to cause similar biases due to fright behaviour. However, visual surveys of fish larvae are not possible in most Australian lowland rivers due to their characteristically high turbidities (Boulton and Brock 1999) and the difficulty of observing very small individuals. Therefore, studies of microhabitat use of small fish in lowland rivers are largely limited to active collection techniques, and the potential for fright bias should be considered in the interpretation of these studies.

The SNE method is not intended to be a quantitative collection method and only allows comparisons between samples on a catch per unit effort basis. In contrast, the collections made using the PAE method have been widely interpreted as quantitative measures of absolute fish abundance (Copp and Penaz 1988, Copp 1992a & b, Copp *et al.* 1994, Garner 1996, Gozlan *et al.* 1998, Jurajda 1999). However, Garner (1997) suggested that at least 50 samples were needed for density estimation, and concluded that density estimates generated from PAE samples should be treated with caution due to the high variation in catch between samples. Estimating the absolute density of individuals present in diverse habitats with either the PAE method or the SNE method is fraught with difficulties, since collection efficiency is likely to vary according to variables such as the size of the individuals, water velocity, water depth, structural complexity of the habitats, water conductivity, operator experience and the voltage selected (Copp and Garner 1995, Reynolds 1996, Garner 1997). Whilst it is possible that the SNE method could be used as a quantitative method by placing a flow meter in the mouth of the net to measure the volume of water sampled, there remains a need for thorough evaluation of electrofishing methods for the quantitative collection of larval and juvenile fish.

Overall, the SNE method appears to be a relatively effective method for the collection of larval and juvenile fish in lotic freshwater environments. The SNE method is not intended as a replacement for the PAE method, but rather, as an alternative whose utility will depend upon the design of the study. The PAE method is most often used for assessments of habitat use using the randomised point abundance sampling strategy. The SNE method has not been used in this way, and may not be suitable for this type of study. So far, use of the SNE method has been restricted to stratified sampling designs, where samples are taken from pre-defined habitat types that are compared (see Chapter 4 and 7). The SNE method is suggested as an improvement over the PAE method in its ability to immediately capture shocked individuals, lessening the likelihood of escape. This may be especially important in lotic systems with low densities of small fish.

This chapter forms the basis of King, A.J. and Crook, D.A. (in press). Evaluation of a sweep net electrofishing method for the collection of small fish and shrimp in lotic freshwater environments. *Hydrobiologia*.

Chapter 4: Ontogenetic Patterns of Habitat Use by Fish within the Main Channel

4.1 Introduction

Many animals undergo changes in their use of food and habitat resources through ontogeny, since the size of an individual influences both its capacity to utilise resources and the nature of its interactions, such as competition and predation (Werner and Gilliam 1984). Ontogenetic niche shifts in both diets and habitat use, have been extensively studied in aquatic communities (Werner and Gilliam 1984). Amphibians, for instance, often exhibit major changes in habitat use and diet, as they metamorphose from tadpoles into frogs (Wilbur 1980). Most species of fish, whether they are marine, riverine or lacustrine, also exhibit major ontogenetic habitat changes (Werner and Gilliam 1984, Wooton 1998). For example, most coral reef fishes have pelagic larval phases and then "settle" out onto reef environments as juveniles (Leis 1991).

In rivers, a number of studies have documented ontogenetic habitat changes by fish within the main channel environment (eg. Scott and Nielsen 1989, Copp 1990, Schiemer *et al.* 1991, Sempeski and Gaudin 1995, Watkins *et al.* 1997). A number of rheophilic species drift into shallow inshore bays as young larvae then move to gravel banks as older larvae and juveniles, whereas eurytopic species drift into inshore bays as young larvae and remain there throughout their early development (Schiemer and Spindler 1989, Schiemer *et al.* 1991). Darters (Percidae) spawn in flowing riffle environments where the eggs develop in interstitial spaces among stones, and then upon hatching, the larvae drift downstream to pool habitats where they feed and develop (Paine 1984). Not all species exhibit ontogenetic habitat change however; some cyprinids remain in shallow littoral habitats as newly hatched larvae until well into their juvenile stages (Garner 1996, Winkler *et al.* 1997). Ontogenetic habitat preferences for one species may also differ among river systems, primarily due to the amount, availability and quality of suitable habitats present (Winkler *et al.* 1997, Jurajda 1999).

Although many adult fish predominantly utilise main channel habitats of floodplain rivers, it is widely accepted that the inundated floodplain environment provides an important

spawning and larval nursery habitat for many species (Welcomme 1985, Junk *et al.* 1989, Humphries *et al.* 1999). However, the main channel environment in large rivers is also used by a number of species for spawning and recruitment. For example, a number of salmonid species spawn in gravel beds in the main channel, and many cyprinids lay adhesive eggs on submerged vegetation in the main channel of rivers (Balon 1975, 1981). Native fishes of the Murray-Darling Basin are widely thought to require periods of floodplain inundation for successful spawning and recruitment in floodplain rivers; this has been termed the 'flood recruitment model' (FRM) (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992, Harris and Gehrke 1994, Schiller and Harris 2001). However, there is little direct evidence to support this conclusion (see review by Humphries *et al.* 1999). Recent studies have established that larvae of a number of species regularly occur in the main channel of two floodplain rivers (Humphries and Lake 2000, Humphries *et al.* in press). A number of these species were also shown to both spawn and recruit during the low flow period in the main channel. This led to the development of the 'low flow recruitment hypothesis' (LFRH), which suggests that some species take advantage of the predictable and extended low flow period to spawn, allowing their larvae access to the increased concentrations of small prey in riverine habitats such as backwaters (Humphries *et al.* 1999). However, apart from the LFRH, fish recruitment in the main channel environment in the Murray-Darling Basin has received comparatively little attention by management or in the scientific literature.

In systems with a high diversity of fishes, assemblages often exhibit a wide variety of recruitment and spawning strategies (Welcomme 1985) and presumably may also exhibit a high diversity of ontogenetic habitat strategies. A variety of strategies in the ontogenetic habitat changes in a fish assemblage may help to ameliorate the effects of predation and interspecific competition for scarce resources (Werner and Gilliam 1984). The number of native fish species in the Murray-Darling Basin has been considered low, when compared with other river systems throughout the world (Lake 1971, Harris 1984, Allen 1989; but see Lake 1995, Gehrke and Harris 2000). The diversity of ontogenetic habitat strategies may therefore, also be small compared with more species-rich northern hemisphere systems. However, to date, the ontogenetic habitat requirements of the Basin's fish fauna remain largely unknown.

This chapter aims to establish which species can spawn and recruit in the main channel of a floodplain river, and to determine the ontogenetic habitat preferences of these species within the main channel environment.

4.2 Materials and Methods

Study sites

The study was conducted in the lowland reaches of the Broken River in north-east Victoria, Australia, a tributary of the Goulburn River (Figure 2.1 and 2.2). A general description of the river is given in section 2.2. Sampling was conducted at three sites (Upper site: 36°31'30''S, 146°57'30''E; Middle site: 36°27'20''S, 145°51'20''E; Lower site: 36°25'45''S, 145°33'45''E) in the lowland portion of the river, downstream of the township of Benalla (Figure 2.2). All sites were on private land, were easily accessible by foot and contained a variety of habitat types. The length of the river sampled varied among sites and sampling trips, from one to three river km, and was dependent on the availability of uncommon habitats such as backwaters within the reach.

Sampling trips

Sampling was conducted every two weeks from October 1998 to the end of January 1999, a total of eight sampling trips. Each site was sampled during the day and the following night, on each sampling trip, and all three sites were sampled within a five-day period. River level was relatively stable and remained confined to the main channel of the river throughout the study period (Figure 2.4). However, the third sampling trip on the 10 and 11 November was interrupted due to persistent heavy rain and a rise in river level. Prior to this, only the day and night samples from one site and the daytime samples from another site were completed. Although the rise in the river did not constitute even a minor flood or connection to the flood plain, sampling for this trip was not resumed, due to the inability to adequately compare the before and after situations.

Sampling gear and design

Sampling was conducted in a habitat specific manner, with samples collected during the day and night from six habitat types: backwaters, still, slow and medium flowing littoral habitats, pools and runs (see Figure 2.5). Fast flowing habitats were rare and usually occurred at natural constrictions in the river and were sampled with a drift net only.

Backwater habitats, commonly termed inshore bays or embayments in European studies (Schiemer and Spindler 1989, Schiemer *et al.* 1991), were generally less than 10 m^2 in size. Typically, backwaters were found at the downstream end of beaches and were characterised by still, shallow water with narrow entrances. Still littoral habitats differed from backwaters, in that they had no restricted entry point, with the entrance at least as wide as the habitat itself. Pool habitats occurred in the middle of the channel with slow flowing deeper water. Run habitats also occurred in the middle of the main channel but were shallower and faster flowing. Water velocity in each habitat was determined by placing the sweep net fixed to the anode pole in the water, and observing any ballooning of the net. If no movement of the net occurred, the habitat was considered 'still', slow ballooning of the net indicated a 'slow' habitat, and rapid ballooning indicated a 'medium' habitat (Copp 1992b). This water velocity estimation technique was evaluated using a Hydrological Services Pty Ltd (Sydney, Australia) current meter (Model No. CMC-200), where three measurements of water velocity were taken within six replicate habitats of each velocity category. Still habitats ranged in speed from 0 to 0.02 m s^{-1} (mean ± SE = 0.02 ± 0.00), slow habitats from 0.07 to 0.22 m s^{-1} (0.16 ± 0.04) and medium habitats from 0.17 to 0.47 m s^{-1} (0.32 ± 0.04).

The majority of sampling was conducted using the sweep net electrofishing (SNE) method, which is described in detail in chapter 3. Hand trawl samples were taken in deeper pool and run habitats, since the SNE method is restricted to wadeable depths. The hand trawl net was similar to a standard zooplankton sampling net, with a 30 cm diameter opening and 250 µm mesh net tapering to a removable collection jar. The net was thrown a distance of 5 m and pulled quickly through the top of the water column, using an attached rope. One replicate sample consisted of five pooled 5 m trawls. A drift net was also set at each site in a naturally constricted part of the river for 3 h during the day and 3 h at night. Drift nets were 1.5 m long, with a 0.5 m diameter mouth opening and were constructed of 500 µm mesh, which tapered to a removable collection jar. A General Oceanics Inc. (Florida, USA) flow meter was fixed in the mouth of each drift net to determine the volume of water filtered.

Five replicate samples of each habitat type were taken using the SNE method, during both the day and night at each site. Five replicate samples were also taken using the hand trawl

method in run and pool habitats only, both day and night. All habitats were selected randomly during the day and then sampled. The same habitats were then sampled again at night. Day samples were always taken between 1000 and 1400 h, and night samples between 2100 and 2400 h. Habitats were not disturbed between the collection of the day- and night-time samples.

A range of habitat characteristics were recorded at each of the sampled habitat replicates. Depth was measured using a graduated pole and recorded as one of five depth categories; 0 – 25 cm, 25 – 50 cm, 0.5 – 1.0 m and > 1.0 m. During daytime sampling, the amount of sun on each habitat was visually estimated and recorded as one of four categories; full sun, part shade, full shade and overcast. The amount of cover was estimated visually and recorded as one of five categories (absent, present (5%), sparse (5 – 25%), medium (25 – 50%) and dense (> 50%)), for submerged woody debris (both branches and tree roots), overhead cover, detritus (decaying leaf litter and small twigs) and submerged vegetation. Temperature and dissolved oxygen were measured with a Horiba U10 Water Quality Checker (Horiba Ltd, Japan) within each sampled habitat. Additionally turbidity, conductivity and pH were measured at three randomly selected sampling points at each site on each sampling trip, also using the Horiba Water Quality Checker. During the study period, water temperature ranged from 13.3 to 27.6 °C (mean ± SE = 22.29 ± 0.09), turbidity from 26 to 110 NTU (57.74 ± 2.40), conductivity from 90 to 250 $\mu S\ cm^{-1}$ (160.00 ± 10.00), pH from 6.60 to 7.83 (7.26 ± 0.04), and dissolved oxygen concentrations from 1.29 to 12.25 $mg\ L^{-1}$ (7.40 ± 0.04).

Preservation and laboratory methods

All samples were preserved in 95% ethanol, and returned to the laboratory where all fish were removed from the samples under a dissecting microscope. Identifications were made using published and unpublished descriptions and keys (Lake 1967b, McDowall 1996, Neira *et al.* 1998, P. Humphries, unpub., see Appendix A). The standard lengths of fish < 10 mm were measured using an eyepiece graticule, and fish > 10 mm were measured using vernier callipers, all to 0.1 mm. Each fish was categorised according to its developmental stage, using categories derived from Ahlstrom *et al.* (1976) and Snyder (1976). These were: protolarvae (no curvature of the notochord in the caudal fin), postflexion (upward flexion of the notochord, caudal fin rays developing), metalarvae

(caudal fin rays developed and pelvic fins beginning to form), juvenile and adult (rays in all fins fully developed). Gambusia larvae, which are born live, were classified into two categories; postlarvae 1 (new born larvae with no pelvic fin buds present) and postlarvae 2 (pelvic fin buds present). Murray cod larvae were also termed postlarvae, due to the advanced development of their fins whilst still retaining their yolk sac.

Data analysis

Frequency distributions were used to describe the differences among each of the six habitat types, using the measured habitat characteristics of depth, illumination, submerged vegetation, overhead cover, detritus and woody debris. The results of substrate type are not shown, since 96% of the habitats sampled were dominated by sand substrates.

A 4-way analysis of variance (ANOVA), with 'site', 'trip', 'day/night' and 'habitat' as fixed factors, was used to describe the patterns of water temperature and dissolved oxygen for all sampled habitats. Residual values of temperature and dissolved oxygen, for each sampling trip within a site and diel period, were used in the analysis to lessen the influence of seasonal differences. Prior to analysis, all data were checked to determine whether they met the assumptions of ANOVA by examining boxplots and plots of means versus variances, however, no transformation was required. All parametric statistics were performed using SYSTAT ™ (Wilkinson 1990).

Apart from the initial description of the fish collected during the study, no further analysis was conducted on fish collected in either the hand trawl or drift net samples. The exception was for Murray cod in drift net samples, as Murray cod larvae were caught only rarely in the other habitats. To determine the diel change in abundance of Murray cod in drift, all drift data were adjusted to a standard volume of filtered water (1000 m^3).

A 3-way ANOVA with 'trip', 'habitat' and 'day/night' as fixed factors, was used to apportion variance for both the total number of larvae and total number of juveniles and adults combined (hereafter juveniles/adults) for Australian smelt, carp, gambusia and rainbowfish, that were captured using the SNE method only. Due to the patchy distribution and low densities of fish captured in the study, zeros dominated the raw data set. To better conform to the assumptions of normality and homogeneity of variance of ANOVA, the

number of fish was averaged across the five replicates of each habitat type, within each site and diel period. The average number of fish per habitat type at each site was then used as a replicate in the ANOVA. Only sampling trips with greater than five individuals of a species present were used in the analysis. The incomplete sampling trip (11 November) was excluded from the ANOVA analysis, since it was unbalanced. Data were also $\log_{10}$ (x+1) transformed before analysis, to better meet the assumptions of ANOVA. Despite this, the data still did not fully satisfy the assumptions of ANOVA and the results of the analysis therefore need to be treated accordingly.

Only Australian smelt, carp, gambusia and rainbowfish of both larvae and juveniles/adults were collected in high enough numbers to analyse their habitat use within the river. Habitat use of these species was established using only those individuals captured with the SNE method. The diel habitat use for both larvae and juveniles/adults of each of the four species was analysed using an index of habitat association (I_{HA}) based on a similar procedure described by Bult *et al.* (1998). The index was calculated using the formula:

$$I_{HA} = \log_{10} (\text{Obs} + 1) - \log_{10} (\text{Avg. R} + 1)$$

Where Obs = total number of fish collected within each habitat category of the observed data, and R = the randomised total number of fish within each habitat category. 'R' was generated using a randomisation procedure, where the observed number of fish per sample were randomly rearranged in the data matrix, and the total number of fish within each habitat type in the randomly generated data is then calculated (Crowley 1992, Potvin and Roff 1993, Sokal and Rohlf 1995). The randomisation procedure was performed using Visual Basic™ (Excel 97™) scripts. The I_{HA} varies around zero, but is not confined to any range. A positive I_{HA} value indicates a positive association with that habitat type, whereas a negative value indicates a negative association. To calculate the significance level of the I_{HA}, the rank of each of the observed data values was established within the generated randomised distribution (Potvin and Roff 1993, Sokal and Rohlf 1995). A total of 1000 randomisation runs were used to determine both the I_{HA} and the statistical significance of the observed data. As in the ANOVA model, only sampling trips where the larvae or juveniles/adults of a particular species were present were used in the analysis. The third sampling trip was also included in this analysis where appropriate. This distribution-free

randomisation approach to the analysis allowed all data to be considered in the model and did not require the strict assumptions of other statistical designs. The statistical significance of ontogenetic habitat changes was determined using chi-squared analysis, using individuals captured with the SNE method only.

Only significant habitat associations were then further analysed to determine whether each species was associated with particular characteristics of those habitats where positive associations were found. The characteristics of the used habitats for each species at both the larvae and juveniles/adult stages were again analysed by an I_{HA} and the statistical significance tested using the randomisation procedure, as described above. Each habitat variable was analysed separately for both day and night. Where fish were significantly associated with two habitats, these were analysed separately. For the illumination variable, samples that were recorded as overcast were excluded from the analysis. Since very few samples of greater than sparse submerged vegetation, overhead cover and detritus occurred within the whole data set (Figure 4.1), these categories were combined for the analysis leaving only two categories, absent and present. Since the temperature and dissolved oxygen data were continuous variables, linear regression was used to determine whether there was any relationship between either dissolved oxygen and temperature and the habitats that larvae were associated with. This analysis was performed on the residual values of temperature and dissolved oxygen, for each sampling trip within a site and diel period.

4.3 Results

Habitat descriptions

Each of the six habitat types differed according to the measured habitat characteristics (Figure 4.1). Backwaters and the three littoral habitats were generally less than 50 cm deep, while runs and pools were generally between 25 – 50 cm and 50 – 100 cm, respectively. Illumination varied little between the six habitat types, however pool and run habitats had a slightly higher proportion of habitats in full sun than backwaters and littoral habitats. Submerged vegetation, overhead cover and detritus were uncommon in medium littoral, pool and run habitats but were in higher densities in backwaters, still and slow littoral habitats. The amount of woody debris was not consistently higher in any of the habitat types, but was variable among the samples.

Temperature patterns differed significantly only between the interaction of 'day/night' and the 'habitat' type ($P < 0.001$, Table 4.1, Figure 4.2a). During the day, backwaters were significantly warmer than most other habitats ($P < 0.05$). However at night, medium littoral, pool and run habitats, were significantly warmer than backwater habitats ($P < 0.05$). On average, water temperature varied little between day and night in the three littoral habitats.

Dissolved oxygen varied significantly with 'habitat' type ($P < 0.001$) and also with an interaction between 'day/night' and 'habitat' ($P < 0.001$, Table 4.1, Figure 4.2b). Dissolved oxygen concentrations were on average significantly lower in backwaters, than in the other habitats ($P < 0.001$). During the day, there was little difference in dissolved oxygen concentrations among the six habitat types, however at night, significantly lower concentrations occurred in backwaters than the other habitat types ($P < 0.001$). The pattern of dissolved oxygen concentration among habitat types differed significantly among the three sites ($P < 0.001$), primarily due to differences between backwater habitats at each site. Dissolved oxygen concentrations in backwaters were on average lower at the lower site, than backwaters at the other two sites and among the other habitat types at all three sites ($P < 0.05$). A three way interaction between, site, trip and habitat also occurred, but explained little of the total variance (Table 4.1).

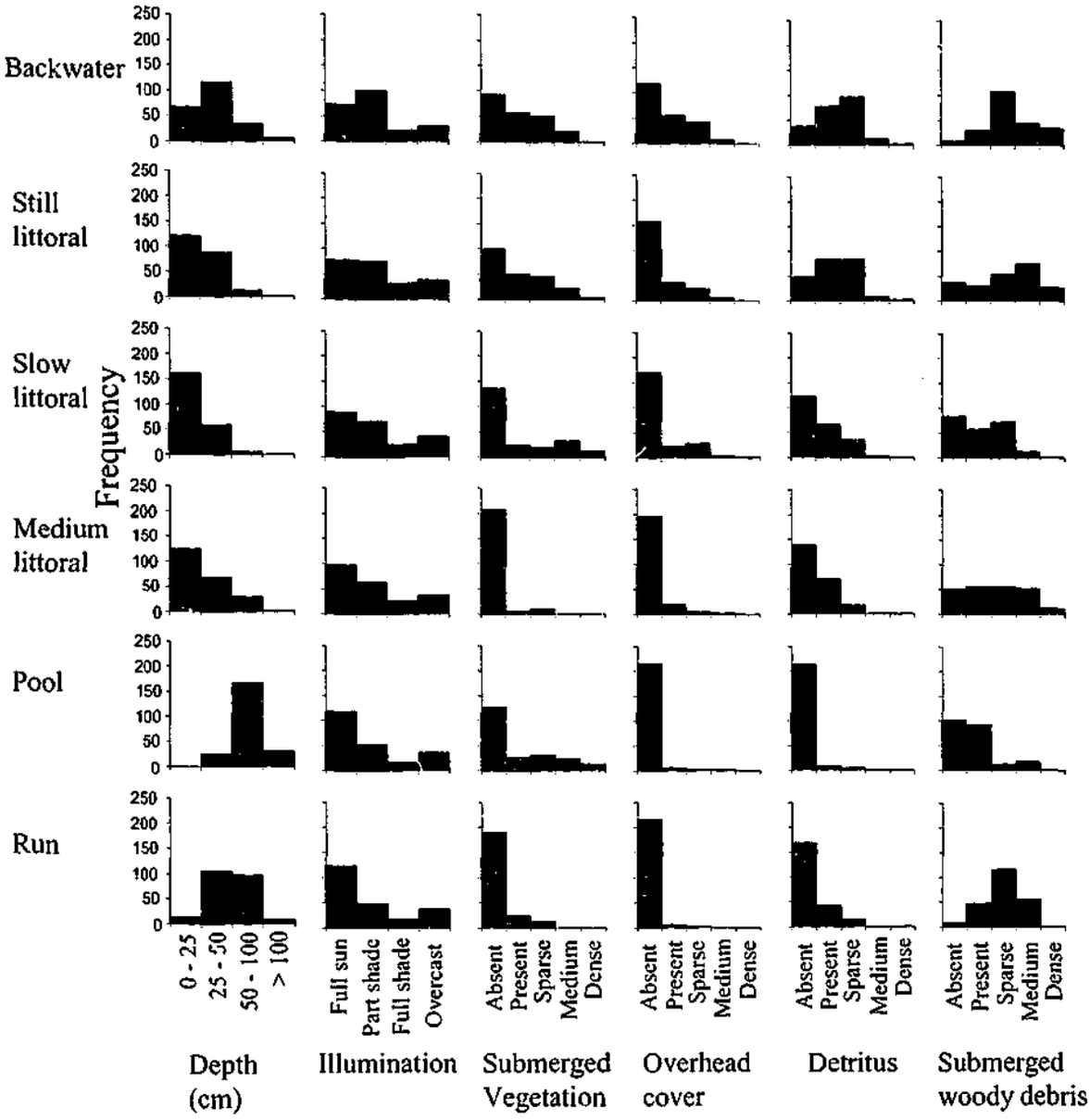


Figure 4.1: Frequency distributions of measured habitat characteristics of depth, illumination, submerged vegetation, overhead cover, detritus and woody debris in each of the six habitat types.

Table 4.1: Mean squares and significance levels for results of 4-way analysis of variance on residuals of temperature and dissolved oxygen, with 'site', 'trip', 'day/night' and 'habitat' as factors. *** = P < 0.001.

		Mean square	
Factor	df	Temperature	Dissolved oxygen
Site	2	0.094	0.054
Trip	6	0.094	0.054
Day/night	1	0.094	0.054
Habitat	5	0.073	2.807 ***
Site * Trip	12	0.094	0.054
Site * Day/night	2	0.094	0.054
Site * Habitat	10	0.118	1.340 ***
Trip * Day/night	6	0.094	0.054
Trip * Habitat	30	0.086	0.256
Day/night * Habitat	5	4.660 ***	1.838 ***
Site * Trip * Day/night	12	0.094	0.054
Site * Trip * Habitat	60	0.106	0.662 ***
Site * Day/night * Habitat	10	0.036	0.102
Trip * Day/night * Habitat	30	0.107	0.110
Site * Trip * Day/night * Habitat	60	0.092	0.110
Error	1008	0.432	0.208

Fish community composition

A total of 1504 larvae and 718 juveniles/adults from nine species were collected throughout the study period (Table 4.2). Seven species were collected as both larvae and juveniles/adults. Of the total fish collected using all three methods, the SNE method captured 61% of larvae and 87 % of juveniles/adults. The SNE method captured a wide size range of fish, from 2.2 mm (carp gudgeon larvae) up to 65.8 mm (juvenile carp) (Figure 4.3a), and was similar to the range collected by the hand trawl method. The SNE method also captured all species as both larvae and juvenile/adults, although drift net sampling was by far the most effective collection method for postlarval Murray cod. The hand trawl method was most effective in capturing larval and juvenile/adult Australian smelt, but they were also captured using the SNE method.

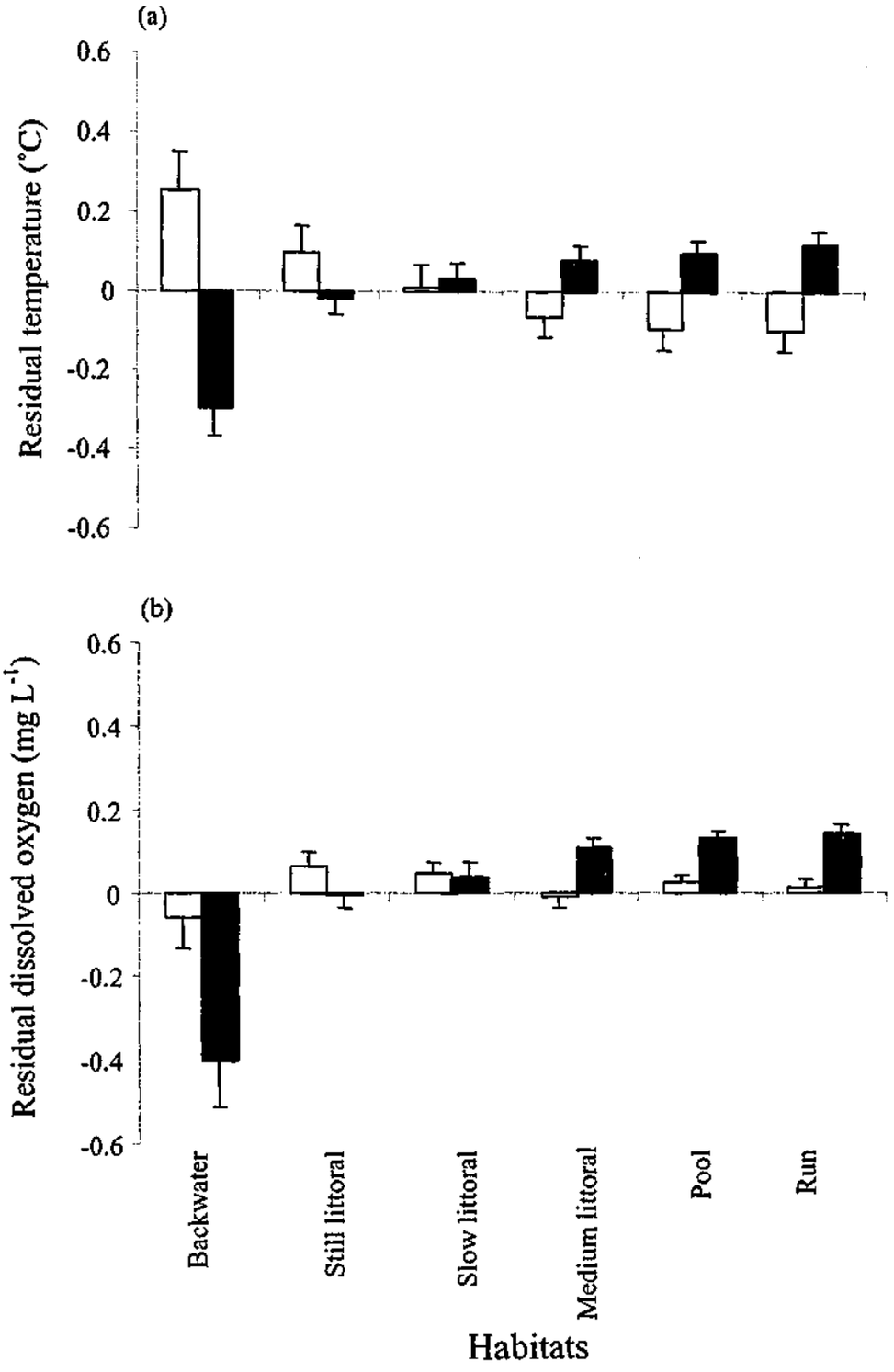


Figure 4.2: Mean (+ 1 SE) residual (a) temperature and (b) dissolved oxygen for each of the six habitat types during the day (clear bars) and night (solid bars).

Table 4.2: Species list and total number of larvae and juveniles/adults (J/A) collected using all three methods and from each sampling trip. SNE = Sweep net electrofishing method, * = Introduced species. Note: The sampling trip on 11 November was interrupted by rising water, and only 1.5 sites were sampled.

Common name	Stage	Size range (mm)	Method			Sampling trips (all methods)								Grand total
			Drift	SNE	Hand trawl	15 Oct	28 Oct	11 Nov	26 Nov	9 Dec	22 Dec	10 Jan	24 Jan	
Australian smelt	Larvae	3.2 – 20.0	0	203	61	18	117	64	42	20	2	0	1	**264**
	J / A	18.1 – 57.0	1	45	83	13	11	3	8	34	24	23	13	**129**
Carp *	Larvae	5.1 – 15.5	19	145	8	0	0	78	24	55	15	0	0	**172**
	J	14.2 – 65.8	1	44	0	0	0	1	18	12	9	5	0	**45**
Gambusia *	Postlarvae	4.3 – 13.4	0	195	0	0	0	0	12	26	34	36	87	**195**
	J / A	11.5 – 37.1	0	309	1	9	5	3	11	33	71	72	106	**310**
Rainbowfish	Larvae	3.9 – 16.1	1	324	1	0	0	0	11	61	64	116	74	**326**
	J / A	10.1 – 34.8	0	152	7	2	1	0	0	3	10	46	97	**159**
Murray cod	Postlarvae	7.8 – 10.0	483	12	11	0	0	1	72	421	12	0	0	**506**
	J	19.0	0	1	0	0	0	0	0	0	0	1	0	**1**
Carp gudgeons	Larvae	2.2 – 5.9	2	35	2	0	0	0	2	2	6	1	28	**39**
(3 sp.)	J / A	11.6 – 44.9	1	62	0	22	6	4	4	4	4	7	12	**63**
Redfin perch *	Larvae	6.7 – 10.0	0	2	0	2	0	0	0	0	0	0	0	**2**
	J	22.1	0	1	0	0	0	0	1	0	0	0	0	**1**
Mountain galaxias	J / A	32.5 – 55.8	0	9	0	1	1	0	1	1	2	1	2	**9**
River blackfish	J / A	19.9	0	1	0	0	0	0	0	1	0	0	0	**1**
		Total larvae	505	916	83	20	117	143	163	585	133	153	190	**1504**
		Total J / A	3	624	91	47	24	11	43	88	120	155	230	**718**
		Total no. of samples	45	1350	450									
		No. of fish per sample	11.29	1.14	0.39									

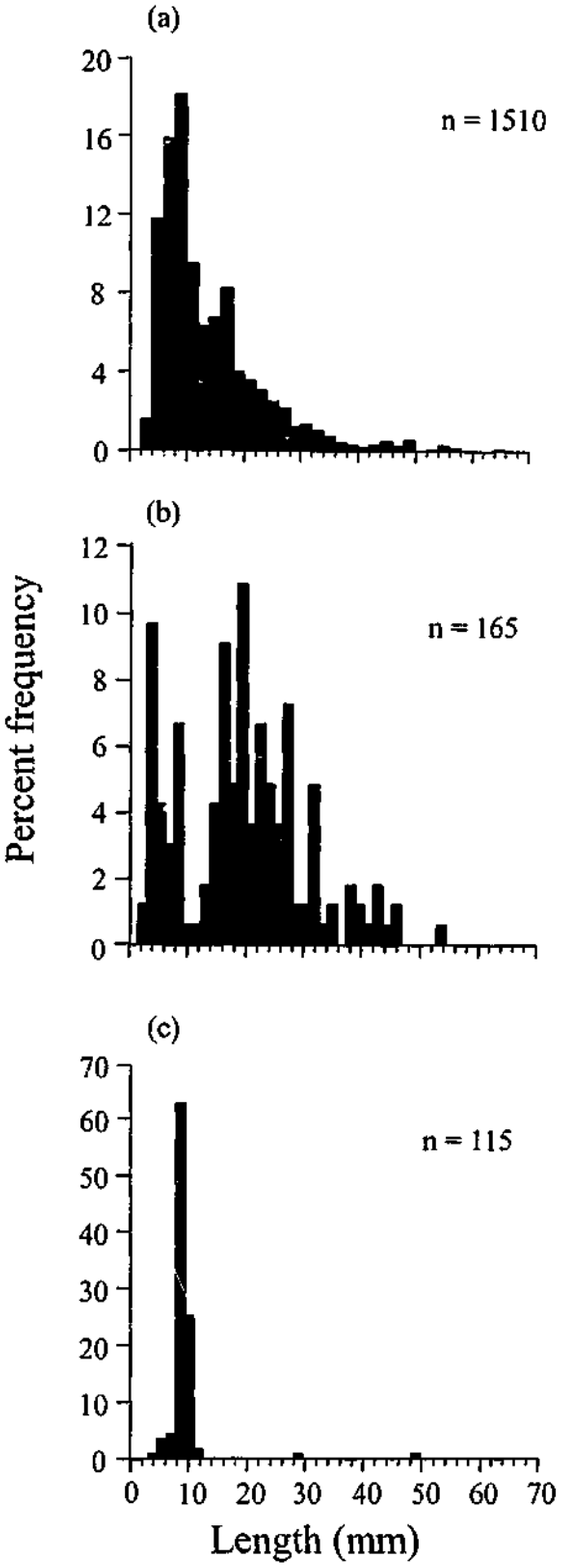


Figure 4.3: Length (mm) frequency distributions of all fish captured using the (a) SNE method, (b) hand trawl method and (c) drift net.

Analysis of variance indicated that the abundance of Australian smelt, carp, gambusia and rainbowfish as larvae and juvenile/adults, varied significantly among habitat types ($P < 0.001$), with the factor 'habitat' contributing the most variance in the majority of cases (Table 4.3). The abundance of most species also differed significantly among sampling trips ($P < 0.01$, Table 4.2 and 4.3), although this was not the case for larval and juvenile carp, or for larval and juvenile/adult Australian smelt. For most developmental stages and species collected, there was little difference in abundance between day and night, except for juvenile/adult Australian smelt and larval rainbowfish. A greater abundance of juvenile/adult Australian smelt was captured at night than during the day ($P < 0.001$), whereas a greater abundance of rainbowfish larvae was captured during the day than at night ($P < 0.001$).

Habitat use

Since for most species 'habitat' contributed the most to the variation in numbers of larvae and juvenile/adults, patterns of abundance among habitat types were examined in further detail using the index of habitat association. Significant positive associations with backwater habitats were found for larvae of Australian smelt, carp and gambusia, during the day and night ($P < 0.01$, Figure 4.4) and for rainbowfish at night ($P < 0.05$). Larvae of rainbowfish were also positively associated with still littoral habitats during the day and night ($P < 0.01$). Gambusia larvae also showed a significant positive association with still littoral habitats but only at night ($P < 0.01$). Larvae of all species were found to be significantly negatively associated with slow and medium littoral, pool and run habitats to varying degrees.

Table 4.3: Mean squares and significance levels for results of 3-way analysis of variance of total larvae and total juveniles/adults (J/A) of four species, with 'trip', 'day/night' (DN) and 'habitat' as factors. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	Australian smelt				Carp				Gambusia				Rainbowfish			
	Larvae		J/A		Larvae		Juveniles		Postlarvae		J/A		Larvae		J/A	
Sampling trips analysed	15 Oct, 28 Oct, 26 Nov		All except 11 Nov		26 Nov, 9 Dec, 22 Dec		26 Nov, 9 Dec, 22 Dec, 10 Jan		26 Nov, 9 Dec, 22 Dec, 10 Jan, 24 Jan		All except 11 Nov		26 Nov, 9 Dec, 22 Dec, 10 Jan, 24 Jan		All except 11 Nov	
Factor	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS
Trip	2	0.098**	6	0.002	2	0.013	3	0.038	4	0.051**	6	0.100***	4	0.076**	2	0.121***
DN	1	0.034	1	0.024***	1	0.010	1	0.000	1	0.006	1	0.001	1	0.233***	1	0.028
Habitat	5	0.102***	5	0.012***	5	0.051***	5	0.208***	5	0.188***	5	0.286***	5	0.367***	5	0.128***
Trip x DN	2	0.044*	6	0.002	2	0.005	3	0.009	4	0.016	6	0.020**	4	0.015	2	0.006
Trip x Habitat	10	0.016	30	0.001	10	0.005	15	0.028	20	0.013	30	0.026***	20	0.021	10	0.019
DN x Habitat	5	0.016	5	0.006***	5	0.001	5	0.002	5	0.015	5	0.066***	5	0.042*	5	0.011
Trip x DN x Habitat	10	0.013	30	0.002*	10	0.001	15	0.019	20	0.005	30	0.010	20	0.013	10	0.015
Error	72	0.014	168	0.001	72	0.010	96	0.030	120	0.011	168	0.007	120	0.014	72	0.012

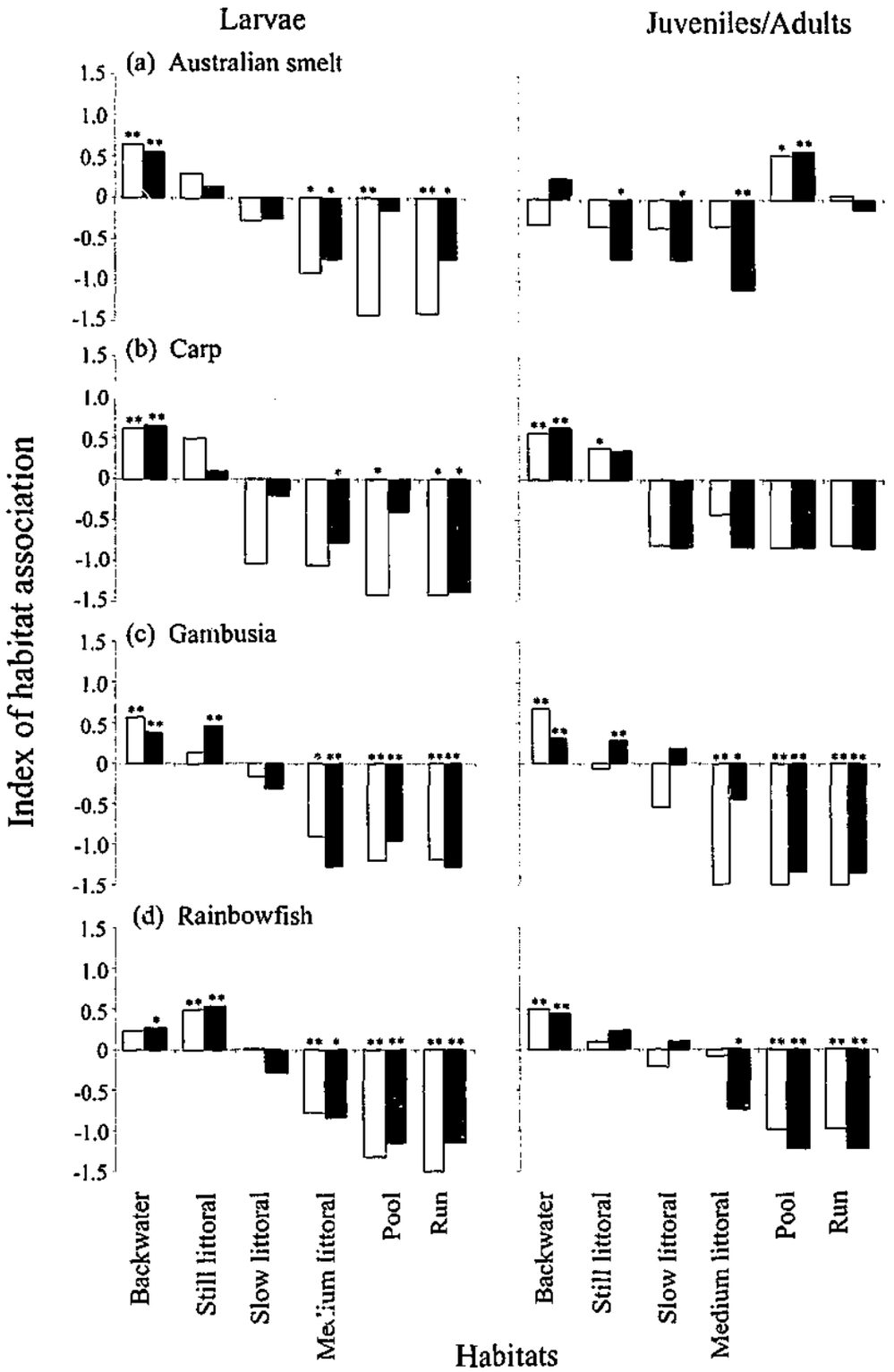


Figure 4.4: Index of habitat association for (a) Australian smelt, (b) carp, (c) gambusia and (d) rainbowfish as larvae and juvenile/adults for each of the six habitat types during the day (clear bars) and night (dark bars). *Significance tests based on randomisation* distributions (see text for details). * = $P < 0.05$, ** = $P < 0.01$.

Similar to the habitat use shown by their larvae, juvenile carp, juvenile/adult gambusia and rainbowfish were all positively associated with backwater habitats (Figure 4.4, $P < 0.01$). Juvenile carp and gambusia also showed significant associations with still littoral habitats during the day ($P < 0.05$) and night ($P < 0.01$), respectively. Australian smelt was the only species to show a significant habitat change with development, shifting from a positive association with backwater habitats as larvae, to a positive association to pools as juvenile/adults (Figure 4.4a). Gambusia and rainbowfish juvenile/adults were generally significantly negatively associated with medium littoral, pool and run habitats.

The development stage of each fish was used to explore whether there were any finer ontogenetic changes in habitat associations. Of the four species, only Australian smelt was found to significantly change its habitat use throughout ontogeny ($\chi^2 = 130.069$, $P < 0.001$, Figure 4.5), from backwater habitats as larvae and then moving into pools as juvenile/adults. Gambusia and rainbowfish were predominantly associated with backwaters and still littoral habitats throughout all life history stages (gambusia: $\chi^2 = 0.658$, $P > 0.05$; rainbowfish: $\chi^2 = 5.06$, $P > 0.05$; Figure 4.5c and d). Carp did not show any significant change of habitat throughout the stages of development captured in the present study ($\chi^2 = 0.608$, $P > 0.05$, Figure 4.5b), however carp protolarvae occurred throughout all six habitat types, while the older stages of larvae and juveniles were predominantly found in backwaters and still littoral habitats. Although adult carp were not targeted in this study, previous studies in the Broken River have shown adult carp to use mainly pool and run habitats (Crook *et al.* 2001), demonstrating a significant ontogenetic habitat change for this species.

Murray cod larvae were rarely found in the littoral habitats commonly used by the other species (Figure 4.6a). They were the only species found to drift downstream as larvae in large numbers (Table 4.2), predominantly at night (t-test, $P < 0.01$, Figure 4.6b). Only one juvenile Murray cod was captured during the study, and therefore it was impossible to determine the habitat use of older fish.

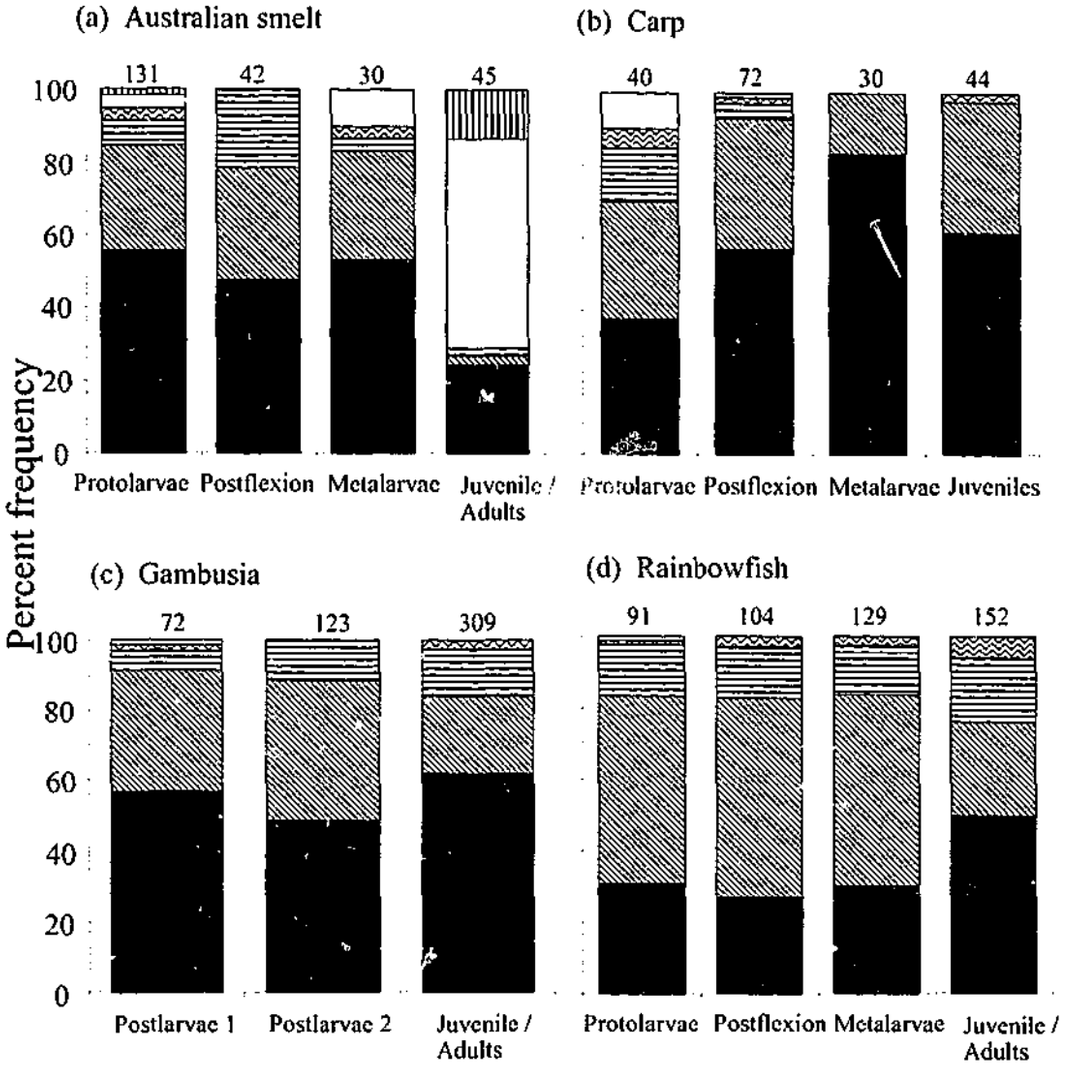


Figure 4.5: Percent frequency of habitat use for each developmental stages of (a) Australian smelt, (b) carp, (c) gambusia and (d) rainbowfish. ■ Backwaters, ▨ Still littoral, ▤ Slow littoral, ▩ Medium littoral, □ Pool, ▥ Run. Number above each bar indicates number of individuals per developmental stage.

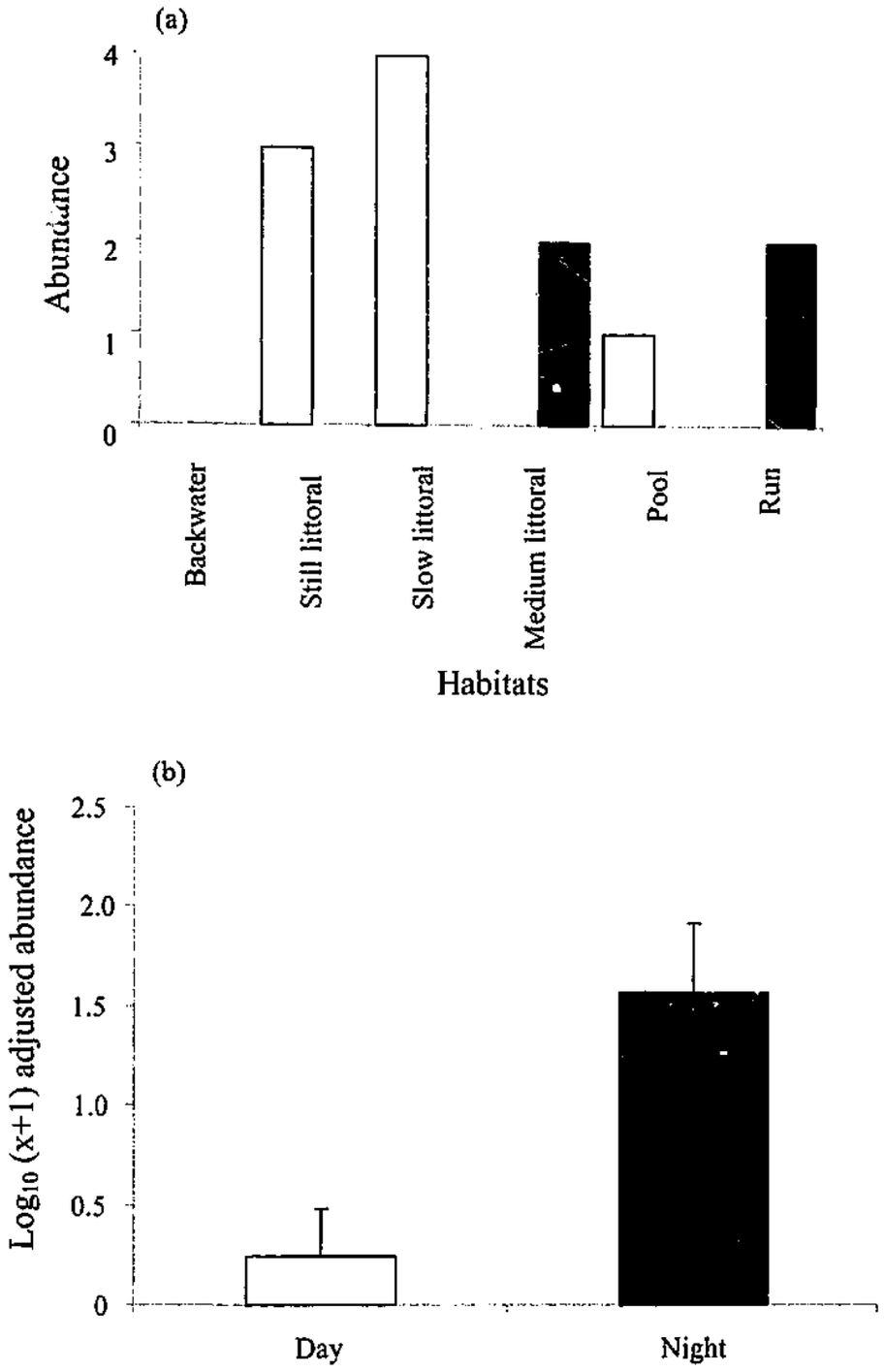


Figure 4.6: (a) Abundance of Murray cod larvae captured using the SNE method in each of the six habitat types during the day (clear bars) and night (solid bars), and (b) adjusted abundance of Murray cod larvae captured in drift net samples during the day (clear bars) and night (dark bars). Drift abundances have been standardised to the number of fish per 1000 m^3.

Association with characteristics of utilised habitats

In general there were few significant associations with the characteristics of the habitats utilised by the four species (Table 4.4). At night larval Australian smelt and juvenile/adult Australian smelt, were positively associated with deeper (50 - 100 cm) habitats, of either backwaters or pools, respectively ($P < 0.05$). Carp larvae showed a significant positive association with shallow (< 25 cm) backwaters during the day and night ($P < 0.01$). Juvenile carp showed no association with any depth class of backwaters or still littoral habitats during the day, but were associated with shallow backwater habitats at night ($P < 0.01$).

Gambusia larvae showed no association with particular characteristics of backwaters during either the day or night, however at night, when they also used still littoral habitats, they showed a positive association with habitats that contained submerged vegetation (Table 4.4, $P < 0.05$). Juvenile/adult gambusia during the day, were positively associated with backwaters containing submerged vegetation and that did not contain dense woody debris ($P < 0.05$). Larvae of rainbowfish were the only species to show an association with an illumination category, preferring shaded still littoral habitats ($P < 0.01$). At night, rainbowfish larvae were positively associated with deeper (50 – 100 cm) backwaters containing overhead cover ($P < 0.01$) and dense woody debris ($P < 0.05$). Although there were a few significant regressions found between temperature and dissolved oxygen and the number of individuals of each species and stage, the variance explained in each regression was extremely low and so was considered to be of little ecological significance (Table 4.4).

Table 4.4: Index of habitat association values for depth, illumination, submerged vegetation, overhead cover, detritus and woody debris, and regression results for temperature and dissolved oxygen, only for significant positive habitat associations for larvae and juvenile/adults (J/A) of Australian smelt, carp, gambusia and rainbowfish. Significance tests for index of habitat association results based on randomisation distribution (see text for details). Significance tests (adjusted r^2) for regression based on normal distribution. BW = Backwater, St. L = Still littoral. * = P < 0.05, ** = P < 0.01, *** = P < 0.001. Significant values also shown in bold.

		Australian smelt				Carp					Gambusia						Rainbowfish				
		Larvae		J/A		Larvae		Juveniles			Larvae			J/A			Larvae			J/A	
		Day BW	Night BW	Day Pool	Night Pool	Day BW	Night BW	Day BW	Day St.L	Night BW	Day BW	Night BW	Night St.L	Day BW	Night BW	Night St.L	Day St.L	Night BW	Night St.L	Day BW	Night BW
Index of habitat association																					
Depth	0-25	-0.10	-0.21	-	-	**0.31****	**0.33****	0.23	-0.13	**0.37****	-0.22	-0.08	0.01	0.01	-0.14	0.14	-0.01	-0.51	-0.07	0.07	-0.19
	25-50	-0.17	-0.19	-0.16	-0.55	**-0.72****	**-0.67****	-0.18	0.17	**-0.57****	0.03	0.04	-0.01	0.02	0.02	-0.21	0.01	-0.03	0.09	-0.16	0.03
	50-100	0.44	**0.45***	0.09	**0.12***	-0.57	-0.35	-0.36	-0.17	-0.35	0.24	0.06	-0.05	-0.09	-0.30	-0.22	0.05	**0.46***	-0.04	0.20	0.17
	>100	-0.61	-0.28	-0.18	-0.61	-	-	-0.07	-	-0.07	0.06	-0.20	-	-0.07	0.59	-0.13	-	-0.11	-	-0.21	-0.30
Illumination	Full sun	0.14	-	0.05	-	-0.23	-	0.05	-0.20	-	-0.14	-	-	0.18	-	-	-0.13	-	-	-0.01	-
	Part shade	-0.10	-	-0.02	-	0.14	-	-0.03	0.21	-	0.18	-	-	-0.17	-	-	-0.21	-	-	0.05	-
	Shade	-0.22	-	-0.14	-	-0.01	-	-0.06	-0.10	-	-0.62	-	-	-0.19	-	-	**0.29****	-	-	-0.12	-
Sub. vegetation	Absent	-0.15	0.04	0.02	0.03	0.03	-0.18	-0.42	0.06	-0.21	-0.04	-0.24	**-0.52***	**-0.33***	-0.18	-0.12	0.02	-0.30	-0.04	-0.46	-0.22
	Present	0.14	-0.07	-0.10	-0.41	-0.02	0.08	0.12	-0.05	0.08	0.02	0.07	**0.34***	**0.14***	0.10	0.08	-0.01	0.09	0.02	0.10	0.06
O'head cover	Absent	0.11	0.12	0.01	0.02	0.14	0.02	0.04	-0.16	-0.04	-0.02	0.10	0.00	0.14	0.11	0.05	0.05	**-0.43****	0.05	-0.08	-0.08
	Present	-0.11	-0.12	-0.06	-0.31	-0.39	-0.03	-0.07	0.27	0.06	0.02	-0.24	-0.30	-0.22	-0.17	-0.13	-0.24	**0.30****	-0.26	0.11	0.11
Detritus	Absent	0.02	-0.23	0.02	0.02	-0.29	-0.30	-0.60	-0.43	-0.05	-0.24	-0.03	-0.24	-0.12	-0.11	-0.30	-0.37	-0.23	**-0.73***	-0.37	-0.26
	Present	0.00	0.03	-0.08	-0.35	0.07	0.06	0.11	0.09	0.01	0.04	0.01	0.05	0.02	0.02	0.06	0.06	0.04	**0.09***	0.04	0.03
Woody debris	Absent	0.72	0.06	-0.14	0.10	0.25	-0.27	-0.06	-0.35	-0.08	0.37	0.03	-0.43	0.57	-0.42	-0.14	-0.21	-0.30	-0.37	-0.07	-0.01
	Present	-0.41	-0.06	0.17	-0.22	0.34	0.37	-0.03	-0.06	0.18	-0.53	-0.16	-0.16	-0.39	-0.16	-0.12	-0.19	-0.72	-0.35	-0.05	-0.60
	Sparse	-0.15	-0.03	-0.10	-0.34	**-0.73***	-0.21	0.03	0.15	-0.14	0.18	0.07	0.04	0.13	0.08	0.17	-0.09	-0.25	0.04	0.00	-0.03
	Medium	0.14	-0.24	-0.11	0.25	0.39	-0.32	-0.19	-0.02	-0.45	-0.30	0.06	0.29	-0.21	-0.14	0.06	0.13	0.15	0.04	0.06	0.15
	Dense	-0.46	0.23	-	-	-0.52	-0.06	0.11	0.08	0.25	-0.68	-0.18	-0.99	**-0.87***	0.11	-0.32	0.11	**0.47***	0.25	0.01	0.18
Regression results																					
Temperature		0.00	0.02	0.00	0.01	0.00	0.00	0.01	0.00	0.00	**0.05***	0.01	0.00	**0.14*****	0.00	0.00	0.00	0.03	**0.09****	0.00	0.00
Dissolved oxygen		0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.00	**0.15*****	0.00	0.02	0.00	**0.03***	0.01	0.01	0.00	0.00	0.00

4.4 Discussion

Occurrence and habitat use of larvae and juveniles in the main channel

It has long been assumed, especially within the management literature, that successful recruitment of native fishes in the Murray-Darling Basin is linked to periods of floodplain inundation (Lake 1967a, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Harris and Gehrke 1994). This assumption has stemmed from aquaculture studies (Lake 1967 a & b) and extrapolation of the flood pulse concept (Junk *et al.* 1989) to Australian systems (see review by Humphries *et al.* 1999). The proposed model, termed the 'flood recruitment model' (FRM) by Harris and Gehrke (1994) suggests that some species such as golden perch, rely on floods to trigger spawning, while for other species, such as Murray cod, flooding enhances larval survival and recruitment success. Despite the lack of supporting evidence for the model, it is commonly extrapolated to all regions of the Basin and to all native species (Geddes and Puckridge 1988, Lloyd *et al.* 1989, Schiller and Harris 2001). The importance of the main channel environment for spawning and recruitment has received comparatively little attention. The present study concurs with recent studies (Humphries and Lake 2000, Humphries *et al.* in press), demonstrating that a number of species are able to spawn and recruit successfully within the main channel, without the occurrence of major flooding or access to the flood plain. This study also confirmed that a number of species such as carp gudgeons, Murray cod, carp, gambusia, Australian smelt and rainbowfish are able to spawn and recruit within the low flow period as proposed by the 'low flow recruitment hypothesis' (LFRH) (Humphries *et al.* 1999).

Whilst the majority of species known to occur within the Broken River were collected as larvae in the main channel during low flow conditions in this study, a notable exception is golden perch. Although golden perch are abundant as adults in the river (pers. obs., P. Humphries, pers. comm.), no larvae were found in the present study and few have been captured in a longer-term study in the river (Humphries *et al.* in press). The cause of the apparently low numbers of larvae and low levels recruitment for this species in the Broken River is currently unknown. However, its absence during this study may lend some support for the FRM and aquaculture studies, which suggest that golden perch require floods to cue spawning (Lake 1967a, Harris and Gehrke 1994).

Murray cod are also abundant as adults in the Broken River, and were captured in high numbers as larvae in the current study. However, only one juvenile Murray cod was caught. The failure to collect juvenile Murray cod may be explained by two possible mechanisms. Firstly, recruitment into the juvenile population may have failed. However, anglers regularly catch 1+ Murray cod in the river (pers. obs), suggesting that recruitment does not continuously fail. Secondly, the methods used in the present study may not have adequately sampled their preferred habitat. This scenario is more likely, since at present the juvenile Murray cod habitat remains largely unknown, but is thought to be similar to the adult habitat of deep pools with dense large woody debris (Koehn 1997).

The nursery habitats of most species in this study, except Murray cod, were shown to be backwaters and still littoral habitats, as predicted in the LFRH (Humphries *et al.* 1999). Larvae of Australian smelt and carp were found predominantly in backwaters, while the larvae of rainbowfish and gambusia used both backwaters and still littoral habitats. Shallow, still littoral habitats including backwaters, are commonly used by the early life stages of fish in other river systems (Moore and Gregory 1988a, Schiemer and Spindler 1989, Haines and Tyus 1990, Tyus 1991, Sempeski and Gaudin 1995, Wintersberger 1996, Watkins *et al.* 1997). These habitats are thought to be ideal nursery areas, as they provide areas of refuge from velocity (Mann and Bass 1997) and from piscatorial predators (Schlosser 1987, Harvey 1991, Eklöv *et al.* 1994), they typically contain high densities of food (Thorp *et al.* 1994) and have warmer temperatures, enabling faster metabolism and growth of larvae (Garner *et al.* 1998).

Garner *et al.* (1998) found that minnows (*Phoxinus phoxinus*) preferentially used backwater-type habitats if they were more than 1 °C warmer than the main channel. Water temperatures in backwaters in the present study were on average only marginally higher than the main channel of the river during the day, suggesting that any benefit of using backwaters to increase growth rates is unlikely in this system. However, a future study should include continuous temperature recordings for both backwaters and main channel habitats, to explore more fully the relative differences between the habitats. Small fish are also thought to actively utilise shallow habitats to avoid predation by larger piscivores (Schlosser 1987, Harvey 1991, Eklöv *et al.* 1994). However, shallow water habitats may also provide an increase in the susceptibility of small fish to avian predators (Power 1987,

Power *et al.* 1989, Harvey and Stewart 1991). Although untested in these systems, the relationship between the use of shallow habitats as an avoidance strategy for predation is likely to be a major factor influencing the habitat associations demonstrated in the present study. The distribution and density of potential prey items may also influence the habitat preferences of larvae and juveniles. Littoral zone habitats, such as backwaters, are known to often contain high densities of zooplankton relative to the main channel environment (Thorp *et al.* 1994). The relationship between the distribution and density of potential prey items and the nursery habitats used by majority of species in this study is tested and discussed in Chapter 6.

The strong nursery habitat associations shown in this study, could be explained by four possible mechanisms: (i) if larvae are considered as passive particles entrained in the water column, they are likely to settle out into depositional habitats with zero or low flow such as backwaters; (ii) that spawning adults actively select nursery habitats for their larvae; (iii) that larvae actively select their own nursery habitats; and finally (iv) that larvae are evenly distributed throughout the river but are not preyed on in shallow habitats. Traditionally larval fish, especially in marine environments, were thought be passive plankters, whose distributions were entirely at the mercy of water currents (Leis 1991). However, there is a growing amount of evidence from marine systems, to suggest that larval and juvenile fish are capable of actively selecting favourable habitats at both large and small scales (Doherty *et al.* 1996, Leis and Carson-Ewart 1998, Öhman *et al.* 1998). The ability of a larva to actively select habitats would depend on its size and robustness, since the size of an individual, amongst other factors, will affect its swimming performance (Lightfoot and Jones 1996, Mann and Bass 1997). However, even small larvae with poor swimming abilities, which may otherwise be passive, may potentially be able to make small vertical or horizontal movements to aid in the selection of favourable nursery habitats. For example, Boehlert and Mundy (1988) suggested that some marine species undergo small vertical movements into surface waters, to facilitate onshore transport into estuarine areas.

In the present study, newly hatched (protolarval) Australian smelt and carp larvae were found to be widely distributed throughout all habitat types, but were strongly associated with backwaters and still littoral habitats at the postflexion developmental stage. This suggests that either postflexion larvae were actively selecting backwaters and still littoral

habitats or that larvae died in all other available habitats. However, the strong nursery habitat association with backwaters and still littoral habitats for larval gambusia and rainbowfish is more likely to be due to adult selection. Since both species prefer still habitats with submerged vegetation and/or woody debris as spawning sites (Backhouse and Frusher 1980, Pen and Potter 1991).

Whatever the mechanism behind the selection of nursery habitats, it is clear from the present study that larvae and juveniles are associated with broad habitat types within the main channel environment of large rivers. A number of studies have demonstrated that larval and juvenile fish respond to microhabitat characteristics (eg. Copp 1992 a & b, 1993, Rincón *et al.* 1992, Copp *et al.* 1994). However, most of these studies do not examine the role of larger scale influences on habitat selection (eg. Poizat and Pont 1996, Kramer *et al.* 1997, Crook *et al.* 2001). In a study of juvenile fish habitats in a lowland river, Poizat and Pont (1996) compared the results of a multi-scale analysis of habitat use with the more classical microhabitat approach. They found that determining habitat preferences based on microhabitat analyses alone did not explain the effect of habitats at larger scales and therefore may incorrectly attribute the observed patterns with microhabitat selection. The present study also found strong associations with identifiable meso-scale habitat features (eg. backwaters and pools), and only a few associations with microhabitat characteristics (eg. depth and the amount of submerged cover).

Diel habitat changes

The diel cycle plays an important role in the movement patterns of fish (Wooton 1998). For example, diel fish migrations, both vertically and horizontally, occur in lakes and billabongs (Emery 1973, Keast *et al.* 1978, Gehrke 1992). Diel changes in habitat associations can be due to increased predation risk (Copp and Juradja 1993), prey availability and accessibility (Baras and Nindaba 1999a) or the regulation of metabolism (Garner *et al.* 1998). In riverine environments, a number of studies have documented movements of small fish into shallow areas at night, and suggested that the movements were undertaken to lower the predation risk from piscatorial predators (Copp and Juradja 1993, Sempeski and Gaudin 1995, Baras and Nindaba 1999b). However, Garner *et al.* (1998) observed movements of small fish from shallow habitats during the day to deeper habitats at night, and suggested that this was due to a trade-off between temperature and

food availability. Tyus (1991) also suggested that the observed diel movements of young Colorado squawfish (*Ptychocheilus lucius*) between backwaters and the main channel were due to a preference for warmer water temperatures.

In the present study, only Murray cod exhibited a strong diel response, with larvae drifting almost entirely at night. The habitat use of the other four dominant species remained fairly consistent between day and night. A small change was observed for gambusia, with both larvae and juvenile/adults positively associated with backwaters during the day, but utilising both backwaters and still littoral habitats at night. However, abundances of juvenile/adult Australian smelt and larval rainbowfish did vary significantly between night and day, suggesting perhaps that subtle diel changes in habitat use, such as use of dense cover or deeper water, may have occurred but were not detected due to gear limitations.

A nocturnal drifting phase has been documented for many fish species in riverine environments (eg. Armstrong and Brown 1983, Brown and Armstrong 1985, Paller 1987, Juradja 1998). A similar pattern of nocturnal drift is also commonly observed for stream invertebrates (see reviews by Waters 1972, Brittain and Eikeland 1988). Despite the widespread occurrence of nocturnal drift by larval fishes, it is not clearly understood why drift occurs. Suggested reasons include feeding behaviour, disorientation at low light levels, accidental entrainment in high currents, predator avoidance and even sampling bias due to gear avoidance (Armstrong and Brown 1983, Brown and Armstrong 1985). In the present study, Murray cod larvae exhibited a strong tendency to drift at night; this has also been observed in longer-term studies in the Broken River (P. Humphries, pers. comm.). Murray cod larvae leave their hatching site in hollow logs or depressions (Rowland 1983) and drift downstream as large larvae with pigmented eyes, large yolk sac reserves and well developed fins (Humphries *et al.* 1999, see also Appendix A). This suggests that instead of drifting accidentally or passively, Murray cod actively choose to drift downstream to juvenile habitats. Further research is still required into the behaviour and cues for the drifting of Murray cod larvae and their juvenile settlement habitat preferences.

Ontogenetic habitat use

Werner and Gilliam (1984) suggested that most fish show marked ontogenetic changes in resource use. The change in resource requirements occurs as organisms increase in age, and usually in size, potentially resulting in size- or stage structured populations (Osenberg *et al.* 1994, MacNally 1995, Olson 1996). Indeed, a number of studies have documented major ontogenetic habitat changes within riverine fish communities (eg. Scott and Nielsen 1989, Schiemer and Spindler 1989, Copp 1990, Schiemer *et al.* 1991, Sempeski and Gaudin 1995, Watkins *et al.* 1997). Schiemer and Spindler (1989) and Schiemer *et al.* (1991) described the early ontogenetic habitat changes of fish assemblages in the Danube River. They demonstrated that during the first few weeks after hatching, all species were associated with sheltered inshore bays. However, with increasing body size and age, rheophilic species migrated out to adjacent shallow gravel banks, while eurytopic species remained in bays throughout ontogeny. Thus, the fish fauna in the Danube River demonstrated two distinct ontogenetic habitat strategies during early life. Watkins *et al.* (1997) found that three cyprinid species in a small English chalk stream exhibited the same overall pattern of ontogenetic habitat shift; with lentic, shallow environments being important for 0+ fishes, whereas deeper, faster areas in the mid-channel were important for $\geq$ 1+ individuals of all three species.

Although the Broken River has a relatively small number of species compared with similar systems in the northern hemisphere, the five dominant species examined in this study exhibited four different ontogenetic habitat use strategies (Figure 4.7). Rainbowfish and gambusia remained in still littoral or backwater habitats throughout all stages of their life cycle. However, Australian smelt and carp demonstrated a significant ontogenetic habitat change with increasing size and development. Australian smelt moved from backwater nursery habitats into pools as juveniles/adults, whereas juvenile carp moved from their backwater nursery habitats into mid-channel habitats as adults (adult habitat use was established from Crook *et al.* 2001). The fourth strategy was demonstrated by Murray cod, whose larvae drifted downstream into an unknown juvenile rearing habitat that is thought

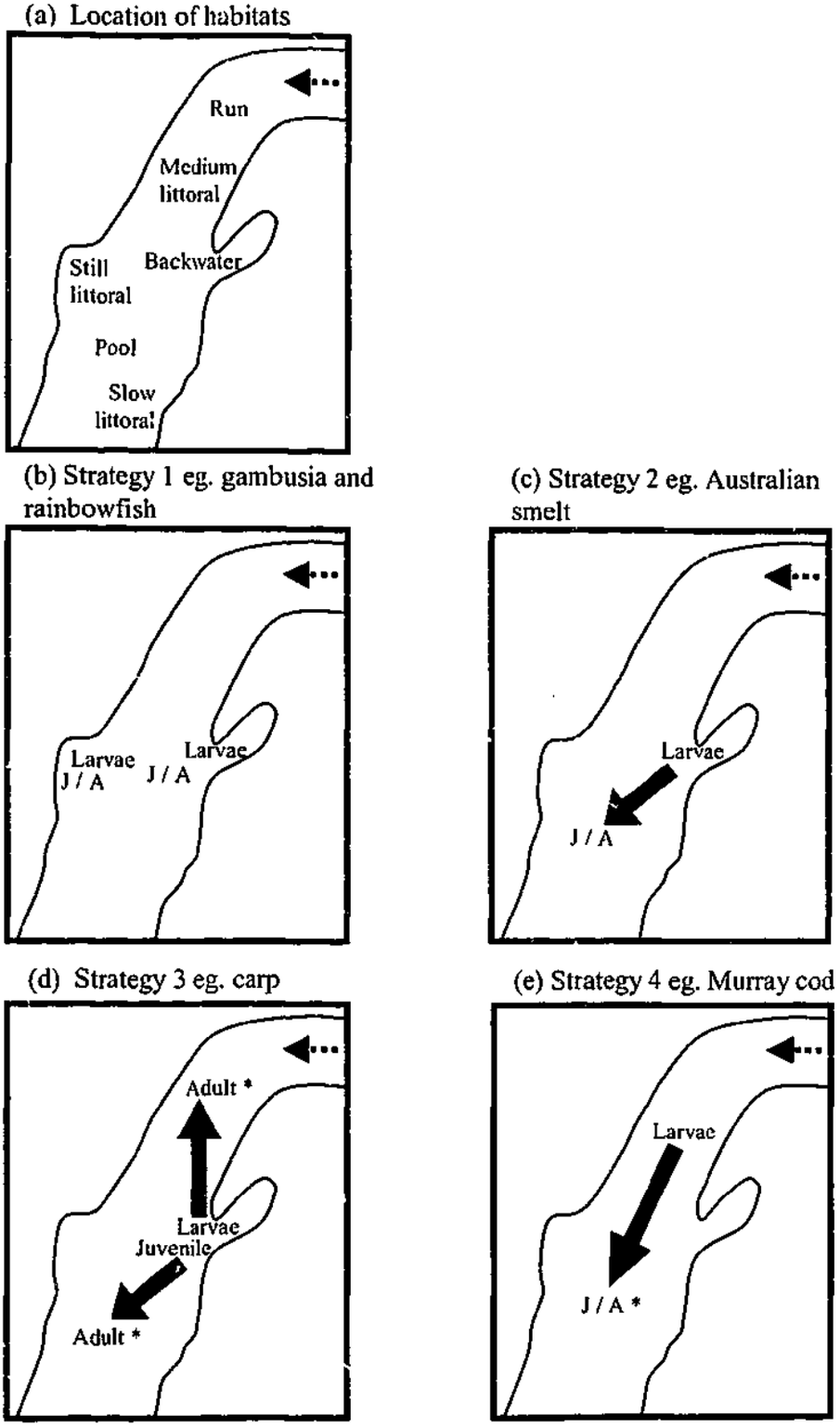


Figure 4.7: Schematic of (a) location of habitats sampled and ontogenetic habitat strategies of (b) Strategy 1 eg. gambusia and rainbowfish, (c) Strategy 2 eg. Australian smelt, (d) Strategy 3 eg. carp and (e) Strategy 4 eg. Murray cod. ◄····· flow direction, * habitat use established from other studies (see text for more detail). ◄ direction of ontogenetic habitat change.

to be similar to the adult preference for deep pools (Koehn 1997). The high diversity of ontogenetic habitat use strategies relative to the number of species in the present study may in part be attributable to the diversity of taxonomic groups represented by the five species. Interestingly, rainbowfish and the introduced species gambusia were not only shown to reproduce at the same time, but also to have exactly the same strategy of ontogenetic habitat use, and were regularly collected together, apparently sharing the same habitats. Interactions between these two species should be examined in more detail in future studies.

Both ontogenetic habitat and diet changes are often either due to, or are simply coincident with, changes in the organism's morphology, such as the transition from larva to juvenile in fish, or metamorphosis from larvae to adults in insects. These have been termed 'genetically fixed behaviours' by Werner and Gilliam (1984) and Mark *et al.* (1989). Ontogenetic habitat changes, are thought to occur in response to assessments of the relative costs and benefits of occupying different habitats, and according to the relative profitability of habitats in terms of foraging, metabolic costs and predation risk (Werner and Gilliam 1984, Wooton 1998). However, ontogenetic habitat shifts may also be induced if unfavourable conditions occur, such as the disappearance of shallow littoral habitats, with changes in water levels or the disappearance of macrophytes in nursery habitats (Copp 1990). Since both the availability of habitats and the habitat preferences of each species changed little with time in the current study, the observed patterns are not likely to be due to the disappearance of preferred habitats in the river. Therefore, the observed patterns appear to be due to either genetically pre-determined habitat selection or a trade-off between prey availability, growth and predators. The influence of prey availability within the sampled habitat types and the ontogenetic diet preferences of the fish, are examined in Chapters 5 and 6.

Chapter 5: Ontogenetic Diet Shifts of Fish within the Main Channel

5.1 Introduction

The early life of fishes is a period of extremely high natural mortality, with often greater than 99% of young fish not surviving to recruit into the adult population (Diana 1995, Trippel and Chambers 1997). Hjort (1914) and May (1974) suggested that the greatest level of mortality occurs through starvation, when young fish start exogenous feeding after their yolk sac is depleted. This is commonly termed the "critical period". During this time, it is assumed that larvae must encounter high densities of appropriately-sized prey to maximise their chance of survival. High densities of small prey are required to sustain larvae, due to their limited search capabilities, arising from a range of physiological constraints such as poor eyesight, small body size, limited swimming abilities and small mouth gape (Bone *et al.* 1995).

From hatching, fish larvae grow quickly, and rapidly change their morphology and physiology, which in turn influences their food choice and processing abilities (Blaxter 1986, Miller *et al.* 1988, Wooton 1998). As larvae grow, they tend to feed on progressively larger and broader range of prey items (Hughes 1997), most likely as a direct result of their increasing mouth gape (Shelbourne 1962, Schael *et al.* 1991). As they grow, larvae and juveniles are thought to optimise their success by changing ecological niches and resources, such as food and habitat; these changes in resource use are termed "ontogenetic niche shifts" (Werner and Gilliam 1984). For some populations, ontogenetic changes can be so marked that the population can be divided into discrete size classes or stages, with each stage potentially playing a substantially different role in community or ecosystem processes (Osenberg *et al.* 1994, MacNally 1995, Olson 1996).

Ontogenetic changes in diet are almost universal amongst fishes (Werner and Gilliam 1984). A large number of studies have documented ontogenetic dietary shifts amongst freshwater fish (eg. Mittelbach 1981, 1984, Winemiller 1989, Wu and Culver 1992, Mol 1995, Garner 1996, Olson 1996, Mérigoux and Ponton 1998, Pusey *et al.* 2000). For example, studies in lakes in the USA have established that small bluegill (*Lepomis macrochirus*) feed primarily on soft-bodied littoral invertebrates, but then switch to limnetic habitats and feed on zooplankton as they grow (Mittelbach 1981, 1984, Werner

and Hall 1988, Osenberg *et al.* 1994). This dietary change is related to a change in habitat, although dietary shifts can also occur within the same habitat. For example, in the littoral zones of lakes, small pumpkinseed sunfish (*Lepomis gibbosus*) feed on soft-bodied invertebrates, whereas larger fish (> 80 mm) feed primarily on snails (eg. Sadzikowski and Wallace 1976, Mittelbach 1984, Osenberg *et al.* 1994).

The co-occurrence of larval fish of different species and ontogenetic stages in the same favourable nursery habitats (eg. Mark *et al.* 1987, Rheinberger *et al.* 1987, Chapter 4), suggests the potential for both inter- and intra-specific competition. However, some studies have demonstrated that interspecific dietary overlaps only occur between newly hatched larvae, with the juvenile period often marking the beginning of dietary specialisation (Mark *et al.* 1987, Garner 1996). Therefore, the larvae or juveniles of co-occurring fish species may be forced through a competitive bottleneck, which in turn may influence the strength of the population in later stages (Werner and Hall 1979, Werner and Gilliam 1984, Persson and Greenberg 1990, MacNally 1995). In European lakes, adult European perch (*Perca fluviatilis*) are piscivorous, preying on roach (*Rutilus rutilus*) and juvenile perch. Juvenile perch, however, are forced to compete with roach for zooplankton in littoral habitats, even though juvenile perch are an inefficient zooplankton feeder compared with roach (Persson 1987a & b, Persson and Greenberg 1990). This type of interspecific competition may therefore mean that prey restrict the recruitment of their predator by decreasing the growth rates of the young predators. This situation is referred to as the "juvenile bottleneck problem" (Werner and Gilliam 1984, Persson and Greenberg 1990, Byström *et al.* 1998).

In the previous chapter, it was demonstrated that Australian smelt larvae shared their nursery habitats with larval and juvenile carp, an introduced species. Similarly, later in the summer, all developmental stages of rainbowfish and the introduced species gambusia utilised the same habitats at the same time. These co-occurrences may potentially give rise to dietary overlap and competition for food resources, especially at the first feeding larval stages, and may result in reduced recruitment for one or both species.

The general composition of the adult diet of most Murray-Darling Basin species is reasonably well understood (eg. McDowall 1996, Kennard *et al.* 2001), although quantitative descriptions are limited (Pusey *et al.* 2000, Kennard *et al.* 2001). However,

the larval diets of only a few species have been studied (Table 5.1). The diet of only one species of native fish has been studied in the wild, albeit in an off-channel billabong (Gehrke 1992). Furthermore, studies conducted under aquaculture conditions have examined only a small number of recreationally important species (Table 5.1). Despite this, it is often assumed that larvae of all species in the Murray-Darling Basin require dense blooms small zooplankton such as rotifers and small crustaceans to sustain them through the larval stages (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989).

Currently, there is little understanding of the importance of the critical first feeding period in early larval survival and successful recruitment, or of dietary changes, resource partitioning and inter- and intraspecific competition during ontogeny of Murray-Darling Basin fishes. The aims of this chapter are to: (i) describe the diets of the larvae and juvenile/adults of common species within the main channel environment; (ii) determine whether the diets differ through ontogeny; (iii) describe other related features of larval feeding, including mouth gape size, size of the prey consumed, presence of yolk sac and their preferred feeding zone in the water column; and (iv) examine dietary overlaps among species and developmental stages, based on the prediction that considerable overlap will occur in the first feeding stages of co-occurring species, and that this overlap will decrease as the juveniles specialise into their adult feeding niches.

Table 5.1: Summary of dietary studies on larvae of Murray-Darling Basin fish. All length values are standard length, except Arumugam and Geddes (1987), where total length is used. * = introduced species, # = first feeding larvae.

Species	Aquaculture/ wild	Age (days)	Length (mm)	Prey consumed	Reference
Trout cod	Aquaculture	21 - 25 #		Copepods, cladocerans, cyclopoids, chironomid larvae	Ingram and Rimmer (1992)
Murray cod	Aquaculture		14 #	Copepods, cladocerans	Rowland (1992)
	Aquaculture		30	Chironomid larvae, corixids	Rowland (1992)
	Aquaculture	27		Chironomid larvae, *Daphnia* and copepods	Lake (1967b)
	Aquaculture	35	17 - 20	Small fish and shrimp	Lake (1967b)
Carp gudgeons	Wild (Murray River, billabong)		< 5 #	Rotifers	Gehrke (1992)
	Wild (Murray River, billabong)		> 5	Calanoid copepods, cladocerans	Gehrke (1992)
	Aquaculture	6 #	3.2 – 3.5	Algae	Lake (1967b)
Golden perch	Aquaculture		4.5 #	*Artemia* nauplii	Arumugam and Geddes (1987)
	Aquaculture	6 #		Small cladocerans, copepods and phytoplankton	Lake (1967b)
	Aquaculture		30	*Daphnia*	Arumugam and Geddes (1987)
Silver perch	Aquaculture		4.6 –5.4 #	Filamentous algae and rotifers	Arumugam and Geddes (1987)
	Aquaculture	6 #		Phytoplankton	Lake (1967b)
	Aquaculture	18	11	Filamentous algae and phytoplankton	Lake (1967b)
Carp *	Wild (Murray River)	9 – 26 #	7 - 15	Cladocerans	Villizzi (1998)
	Wild (Murray River)	42	36	*Phragmites* seeds, cladocerans	Villizzi (1998)

5.2 Materials and methods

Dietary analysis was conducted on the majority of individuals sampled from the main channel habitats of the Broken River (see Chapter 4). A full description of the methodology used to collect the fish is given in section 4.2. Most individuals used for dietary analysis were collected using the two active sampling methods: the Sweep Net Electrofishing (SNE) and hand trawl methods. Active sampling methods were chosen to alleviate the problems of post capture digestion and feeding that may occur if individuals are captured in traps (Bowen 1996). Briefly, SNE samples were collected in six habitat types and hand trawl samples from pool and run habitats, fortnightly at three sites from October 1998 to the end of January 1999 in the Broken River downstream of Benalla. This study collected sufficient fish to allow gut content comparisons for six species: Australian smelt, carp, gambusia, Murray cod, rainbowfish and carp gudgeons. Due to the low abundance of larval Murray cod in both the SNE and hand trawl method samples, dietary analysis was supplemented by 100 individuals randomly selected from drift samples. Since post-capture digestion or feeding may have occurred for the individuals from the drift samples, they were initially analysed separately. However, their diets were found not to differ from the actively sampled individuals (King unpub. data) and so individuals collected using both types of methods were grouped in further analyses. Only small numbers of larval carp gudgeons were captured and were therefore only used in the preliminary descriptions of the diet and not in further analyses.

Dietary analysis

After preservation in the field with 95% ethanol, samples were returned to the laboratory. All samples were sorted, fish identified and developmental stage determined using a dissecting microscope. Only undamaged individuals were used for dietary analysis. Fish identifications were made using published and unpublished descriptions and keys (Lake 1967b, McDowall 1996, Neira *et al.* 1998, Humphries, unpub. data., see Appendix A). The developmental stage of each fish was determined, using categories derived from Ahlstrom *et al.* (1976) and Snyder (1976), based on morphological development of the fish (see descriptions in Chapter 4). The standard lengths of small fish were measured to 0.1 mm using an eyepiece graticule, and those of larger juvenile/adult fish were measured to 0.1 mm using vernier callipers. The greatest width of a fish's mouth (gape size), when viewed from the ventral surface was used to estimate the maximum gape (Arumugam and

Geddes 1987). The gape of each fish was measured to 0.01 mm using an eyepiece graticule. The presence or absence of a yolk sac was also recorded.

Due to the small size of larvae of some species, the entire digestive tract, including the intestine and stomach if present (hereafter referred to as the 'gut'), was used for analysis on all fish, including larger individuals. The small size of the gut and prey required the use of a dissecting microscope with an inverted light source. The entire gut was dissected from each fish in a solution of 95% ethanol, using fine dissecting needles, scalpels and forceps. The dissected gut was blotted on tissue paper and placed in a drop of glycerol on a glass slide. The glycerol acted as a viscous medium for further gut dissection and prey identifications. Each gut was then carefully slit open and the total volume of all prey items noted using the points method (Hynes 1950, Hyslop 1980). The points method provides an indication of the relative volume of the different components in the guts. The method involves assigning the total content of the gut a fullness value, and then giving each prey item a value appropriate to its relative volume in the gut. Identification of prey items were made using Williams (1980), Shiel (1995), Hawking and Smith (1997), and by consulting with experts in relevant taxonomic groups (R. Shiel and J. Hawking, Murray-Darling Freshwater Research Centre, pers. comm.). Prey items were grouped into broad taxonomic categories, with a total of 47 categories defined (see Appendix C). The width of the largest and smallest prey items in each gut were measured to 0.01 mm, using an eyepiece graticule. Only data from fish with non-empty guts were used in any dietary comparisons or statistical analysis, except analysis of average percent gut fullness. The percent frequency of occurrence and the percent by volume of each dietary category were calculated for each developmental stage of each species. The proportional contribution of unidentified material was excluded from all further analyses.

The Shannon-Weiner index of diversity (Pielou 1966) was used to estimate the dietary breadth (Scrimgeour and Winterbourn 1987) of each developmental stage for each species. The index was calculated using the formula,

$$H' = - \sum p_i \ln p_i$$

where p_i is the proportion of resource in the ith class. This was then standardised by calculating evenness (E), using the equation $E = H' / H'_{max}$ (Pianka 1986). Values for E

range from near 0, when the species feeds on a single taxon, to 1, a complete generalist where each prey taxon is ingested in equal proportions.

Schoener's index (T) of overlap (Schoener 1970) was used to calculate the degree of similarity in the diet among all developmental stages and species of fish. The index was calculated using the formula,

$$T = 100 - 0.5\,(\sum | P_{xi} - P_{yi} |)$$

where P_{xi} and P_{yi} are the percentage by points of each dietary category for all pairs of fish samples x, y. Values for T range from 0 for no overlap (no similarity) to 1 for complete overlap (complete similarity), with values of ≥ 0.60 considered biologically significant (Zaret and Rand 1971, Mathur 1977, Wallace 1981).

The proportion by volume of each prey category in five different prey habitat zones: epibenthic, pelagic, both epibenthic and pelagic (hereafter epibenthic/pelagic), surface and other; were used to examine the feeding areas for each developmental stage of each species. The habitat zones for each prey type, shown in Appendix C, were categorised using information in Williams (1980), Merrit and Cummins (1984), Thorp and Covich (1991), Shiel (1995) and consultation with experts in the relevant taxonomic groups (J. Hawking and R. Shiel, Murray-Darling Freshwater Research Centre, pers. comm.). Since unidentified material was excluded from the analysis, the contribution of all prey items in each habitat zone was standardised to sum 100%.

Statistical analysis

The relationship between standard length and gape size, and gape size and width of the largest and smallest prey items, was determined by linear regression using SigmaPlot ™ (SPSS 1997). Analysis of covariance was used to test whether the equations of the regression lines for length versus gape size were significantly different from each other, using SYSTAT ™ (Wilkinson 1990). The slopes of the lines were first tested for parallelism and if there was no significant difference, the intercepts were then tested.

Three-way analyses of variance (ANOVA's) were carried out for each species separately to investigate whether gut fullness differed among 'developmental stages', between 'day

and night', and among 'habitats'. All developmental stages for carp, gambusia and rainbowfish were used in the analyses. Only larval developmental stages were used in the analysis for Australian smelt, due to the significant habitat change by juvenile/adults (see Chapter 4). The habitats used in these analyses, were those where a significant preference was shown in Chapter 4, ie. backwaters and still littorals. Untransformed data were checked for normality using probability plots and box plots, and were found to meet the assumptions of ANOVA. When ANOVA indicated a significant effect, *post hoc* comparisons were made using Tukey's test. All ANOVA's were performed using SYSTAT ™ (Wilkinson 1990).

To examine ontogenetic changes in the diets of all developmental stages of each species three ordinations, using non-metric multidimensional scaling (NMDS) in the software program PC-ORD™ (McCune and Mefford 1999) were conducted. Firstly, an NMDS ordination was used to examine the relationship between the diets of all developmental stages and species, using the mean percent volume data of each dietary category, excluding unidentified material and rare prey items (contributing < 1% to a category). Additionally, two further NMDS's were used to examine whether there was any overlap in the diet of species that occurred in the same habitats at the same time. Australian smelt larvae and all developmental stages of carp co-occurred in backwaters and still littoral habitats, while all stages of gambusia and rainbowfish also co-occurred in backwaters and still littoral habitats (see Chapter 4). The mean percent volume of each prey category of developmental stages and each species within each habitat and day/night category was used in the analyses, ie. creating four values for each stage and species combination. For all three ordinations, the mean percent contributions were log-transformed and the Bray-Curtis similarity measure was used. The multi-response permutation procedure (MRPP) in PC-ORD™ (McCune and Mefford 1999) was used to establish whether there were significant differences in diet between species and stages in all three ordinations, the probability of achieving the result (P) and a descriptor of within-group homogeneity (A) is reported.

5.3 Results

Fish length, gape and prey size

Highly significant linear relationships between standard length and gape size existed for carp, Australian smelt, gambusia, rainbowfish and carp gudgeons across all developmental stages (Figure 5.1, $P < 0.001$). The relationship between length and gape size was significantly different between pairings of carp, Australian smelt, rainbowfish and carp gudgeons (slopes of all pairings: $P < 0.001$, except rainbowfish and carp gudgeons, where $P < 0.05$). The slope of the regression lines for gambusia and rainbowfish, and gambusia and carp gudgeons were not significantly different ($P > 0.05$), but the intercepts of the lines were significantly different from each other ($P < 0.001$). The strong linear relationship between length and mouth gape also held for the larval stages only of all species (Figure 5.2, $P < 0.001$). For all species, the equation of the regression line remained similar whether or not juvenile/adults were included in the data. The slope of the relationship between standard length and gape size for Australian smelt was not as steep as the other species, indicating that Australian smelt at large lengths had relatively small gapes compared to other species (Figure 5.1b & 5.2b). Postlarval Murray cod were much larger than the other species at first feeding, had a much larger gape size than other species at the same length, and had a wider range of gape sizes for a specific length (Figure 5.2f).

The width of the largest prey item versus gape size did not increase at a 1:1 ratio, with all species eating prey considerably smaller than their maximum mouth gape (Figure 5.3). The width of the largest prey item in the gut, increased significantly with larger mouth gapes of carp, Australian smelt, gambusia, rainbowfish and carp gudgeons (Figure 5.3, $P < 0.001$). However, carp, Australian smelt, gambusia and carp gudgeons, ate both large and small sized prey as their gape increased, with no significant relationship observed between width of the smallest prey item and gape size. Conversely, the width of

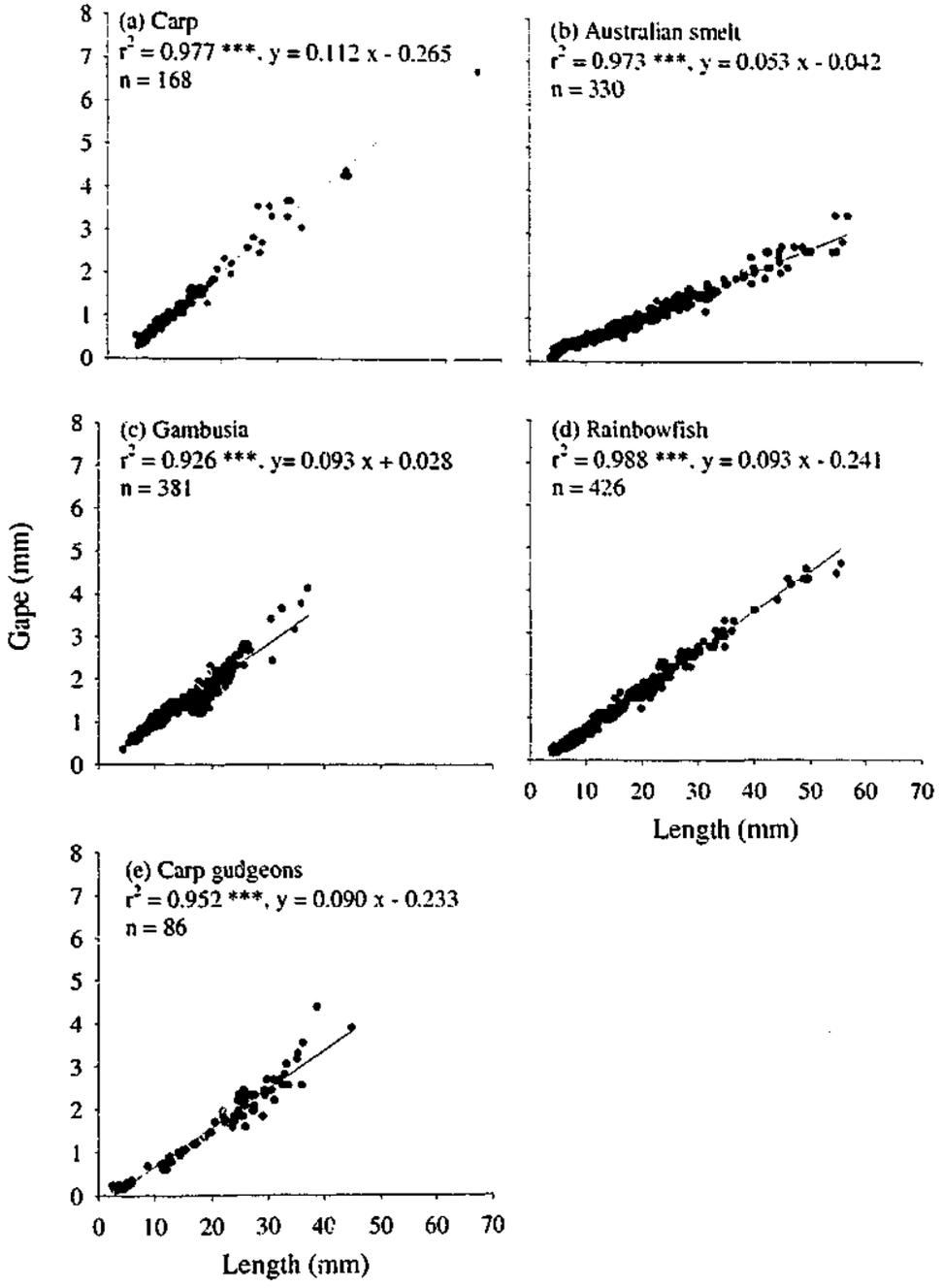


Figure 5.1: Linear regressions for standard length (mm) versus gape size (mm) for all developmental stages (ie. both larvae and juvenile/adults) of (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish and (e) carp gudgeons. *** = $P < 0.001$.

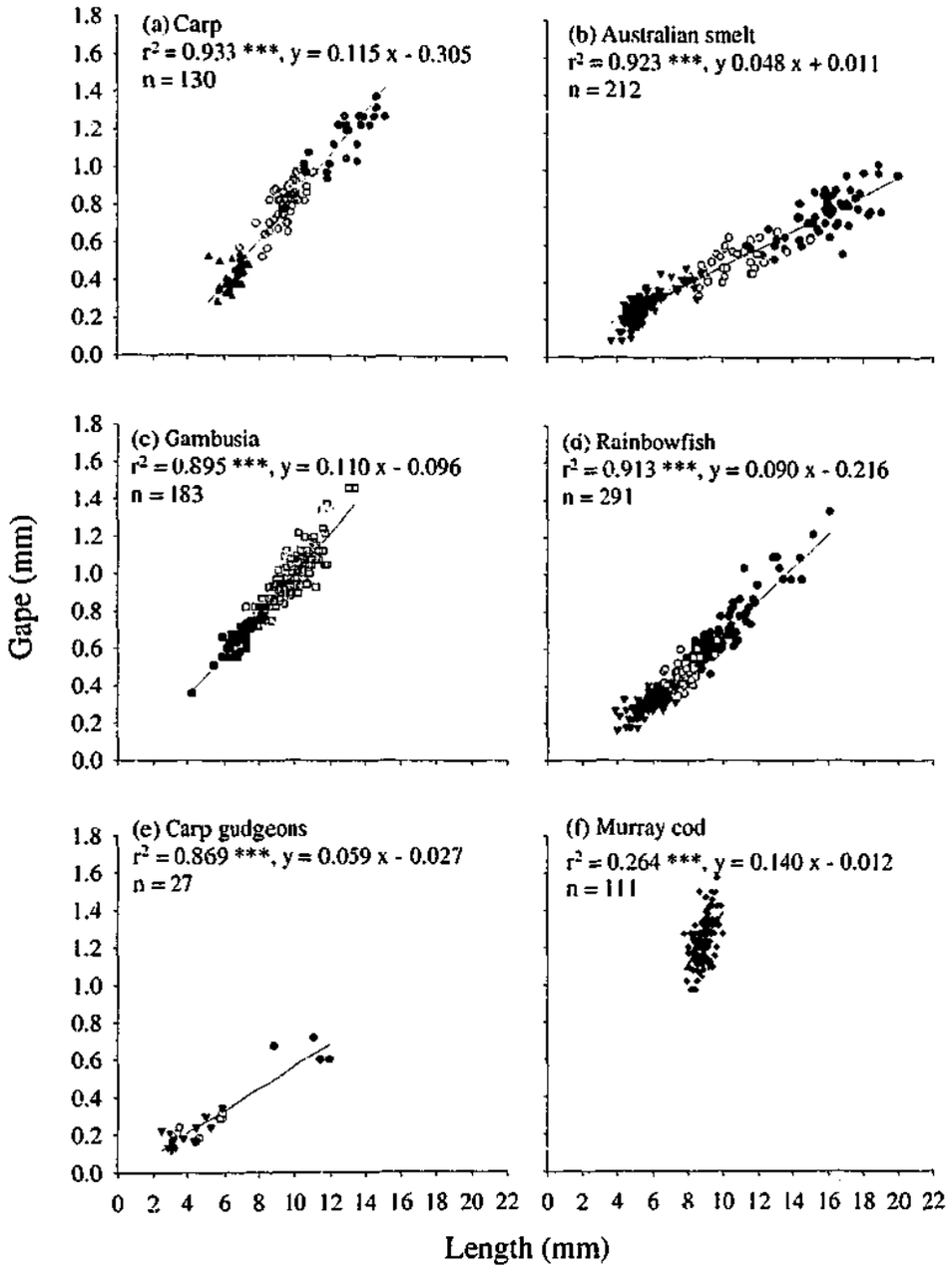


Figure 5.2: Linear regressions for standard length (mm) versus gape size (mm) for all larval stages only of (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish, (e) carp gudgeons and (f) Murray cod. Developmental stages: protolarvae (solid triangles), postflexion (clear circles), metalarvae (solid circles), postlarvae 1 (solid squares), postlarvae 2 (clear squares), postlarvae (solid diamonds). *** = $P < 0.001$.

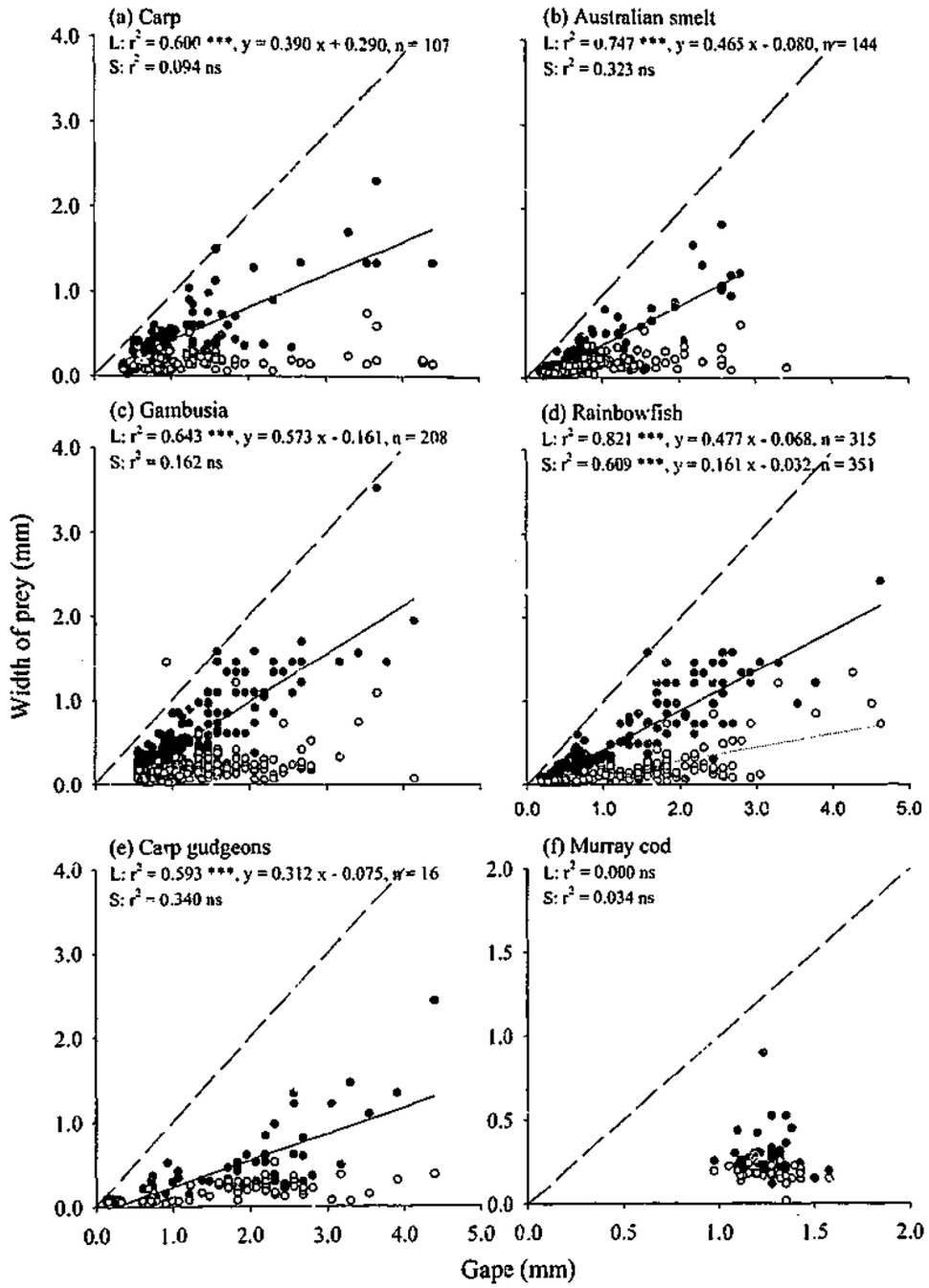


Figure 5.3: Linear regressions of gape size (mm) versus width of largest (solid circles, solid line) and smallest (white circles, dotted line) prey (mm) for all developmental stages of (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish, (e) carp gudgeons and (f) Murray cod. Dashed line represents 1:1 ratio where prey size = gape size. L = regression results for width of largest prey, S = regression results for width of smallest prey. Note different y and x axis scales for Murray cod. *** = $P < 0.001$, ns = non significant. Regression lines and equations only shown for significant results.

the smallest prey in the guts of rainbowfish increased significantly with mouth gape (Figure 5.3d, $P < 0.001$), but there was still a large variation in the size of prey consumed. There was no relationship between mouth gape and either the width of the largest or smallest prey for Murray cod postlarvae (Figure 5.3f, $P > 0.05$).

First feeding, yolk sac presence and gut fullness

A large proportion of protolarval carp (55%), Australian smelt (49%) and carp gudgeons (56%), and postlarval Murray cod (40%) had empty guts (Table 5.2). Rainbowfish was the only species to have 100% of their protolarvae with food present in their guts. Yolk sacs were present in approximately 96% and 76% of carp protolarvae and Murray cod postlarvae, respectively. Additionally, approximately 19% of Australian smelt protolarvae, 44% of carp protolarvae and 60% of Murray cod postlarvae contained food in their guts and also retained a portion of their yolk sac.

The percent gut fullness varied significantly with 'developmental stage', explaining the majority of the variance for carp, Australian smelt, gambusia and rainbowfish (Table 5.3, Figure 5.4, $P < 0.001$). In general, the percent gut fullness increased significantly throughout the development of carp, Australian smelt, gambusia and rainbowfish. A similar increase in the percent gut fullness through ontogeny was also observed for carp gudgeons (Figure 5.4e). The ANOVA showed a significant effect of 'habitat' only for Australian smelt, with greater gut fullness of larvae in backwaters than in still littoral habitats. However, the difference between the two habitats was extremely small (< 1%), and was therefore considered to be of little biological meaning. Only rainbowfish demonstrated any diel pattern in feeding, with significantly greater gut fullness occurring at night (mean = 81.89, SE ± 1.13) than day (mean = 72.60 %, SE ± 1.37) ($P < 0.01$). The average percent gut fullness for Murray cod postlarvae was only 20% (Figure 5.4f).

Table 5.2: Number of fish, range and mean (1 SE) of standard length, mean (1 SE) gape size, number of non-empty guts, percentage of empty guts, percentage with yolk sacs, percentage with yolk sacs and food in gut for each developmental stage of each species. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2, PL = postlarvae.

Species	Stage	Number of fish	Length (mm)		Gape	No. non-empty guts	% fish with empty guts	% fish with yolk sacs	% fish with yolk sac + food
			Range	Mean (SE)	Mean (SE)				
Carp	PR	47	5.12 – 7.44	6.55 (0.07)	0.42 (0.01)	21	55.32	95.74	44.44
	PF	62	6.47 – 11.10	9.34 (0.12)	0.79 (0.02)	60	3.23	3.23	1.61
	M	30	10.61 – 15.49	12.99 (0.25)	1.17 (0.02)	30	0.00	0.00	0.00
	J	41	14.15 – 65.80	23.19 (1.67)	2.43 (0.19)	41	0.00	0.00	0.00
Australian smelt	PR	142	3.17 – 8.78	5.26 (0.09)	0.27 (0.01)	73	49.31	33.80	18.75
	PF	38	7.93 – 15.00	10.30 (0.28)	0.50 (0.01)	28	26.32	0.00	0.00
	M	62	11.35 – 20.01	15.80 (0.26)	0.76 (0.02)	60	3.23	0.00	0.00
	JA	123	18.10 – 57.00	29.97 (0.86)	1.57 (0.05)	123	0.00	0.00	0.00
Gambusia	PL1	59	4.27 – 9.15	6.89 (0.10)	0.66 (0.01)	54	8.47	1.69	0.00
	PL2	128	7.32 – 13.42	9.92 (0.10)	0.99 (0.01)	127	0.78	0.00	0.00
	JA	203	11.47 – 37.10	18.48 (0.30)	1.73 (0.03)	201	0.99	0.00	0.00
Rainbowfish	PR	83	3.90 – 7.32	5.74 (0.09)	0.31 (0.01)	83	0.00	0.00	0.00
	PF	95	4.88 – 9.64	7.41 (0.09)	0.43 (0.01)	95	0.00	0.00	0.00
	M	127	7.32 – 16.10	9.67 (0.15)	0.65 (0.02)	127	0.00	0.00	0.00
	JA	142	10.13 – 55.70	23.49 (0.76	1.98 (0.07)	142	0.00	0.00	0.00
Carp gudgeons	PR	18	2.20 – 5.86	3.63 (0.25)	0.19 (0.02)	8	55.56	50.00	0.00
	PF	7	3.42 – 5.86	4.79 (0.40)	0.24 (0.02)	5	28.57	0.00	0.00
	M	4	8.78 – 11.96	10.83 (0.70)	0.65 (0.03)	4	0.00	0.00	0.00
	JA	59	11.59 – 44.90	25.09 (0.98)	2.00 (0.10)	59	0.00	0.00	0.00
Murray cod	PL	122	7.81 – 10.00	8.91 (0.04)	1.24 (0.01)	73	40.16	76.23	60.21
TOTAL		**1592**				**1414**			

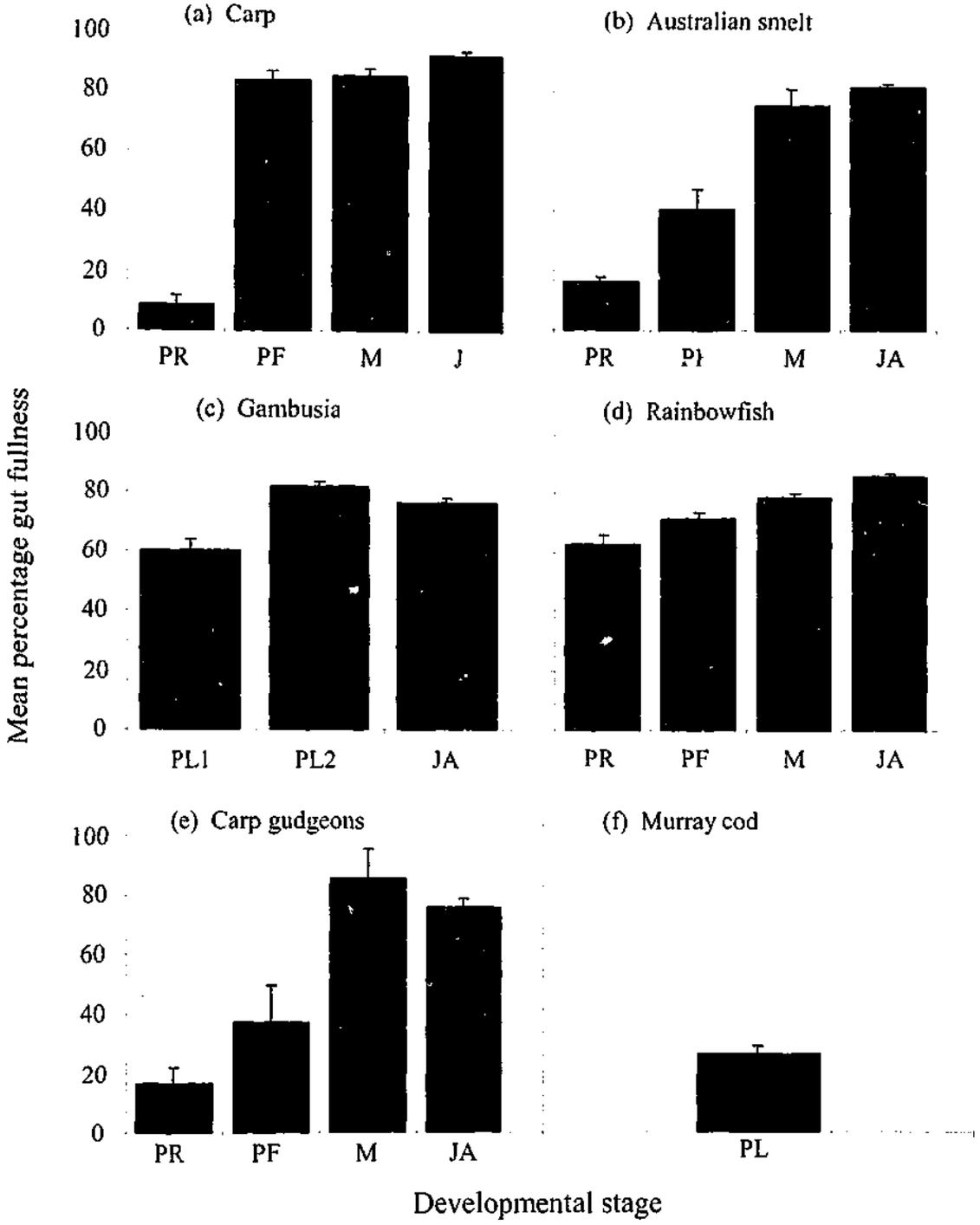


Figure 5.4: Mean (+ 1SE) percent gut fullness for each developmental stage of (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish, (e) carp gudgeons and (f) Murray cod. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2, PL = postlarvae.

Table 5.3: Mean squares and significance levels for results of 3-way analysis of variance with 'developmental stage', 'day/night' (DN) and 'habitat' as factors, on percent gut fullness for carp, Australian smelt, gambusia and rainbowfish. * = P < 0.05, ** = P < 0.01, *** = P < 0.001. Australian smelt ANOVA based on larval stages only.

	Carp			Australian smelt			Gambusia			Rainbowfish		
	df	MS		df	MS		df	MS		df	MS	
Stage	3	43328	***	2	17968	***	2	4316	***	3	3492	***
DN	1	649		1	1306		1	738		1	2186	**
Habitat	1	190		1	3163	*	1	4		1	136	
Stage x DN	3	116		2	1100		2	1450	*	3	672	
Stage x Habitat	3	620		2	1946	*	2	93		3	729	
DN x Habitat	1	1109		1	241		1	1165		1	0	
Stage x Habitat x DN	3	309		2	786		2	571		3	114	
Error	140	277		147	499		308	439		342	269	

Changes in diet composition, breadth and feeding strategy with ontogeny

A total of 1592 fish guts were examined, of which 1414 guts contained food and were therefore used in further analyses (Table 5.2). The relative contribution of the 47 dietary categories varied significantly among both developmental stage and species (Table 5.4, Appendix B). Apart from unidentified material, the most common prey items in the guts were chydorids, chironomid larvae, macrothricids and cyclopoids (Table 5.4). The developmental stages of all species showed generalist feeding behaviours, with no feeding specialization evident (Table 5.4).

Strong dietary changes with ontogeny were evident for carp, Australian smelt, gambusia and rainbowfish (Table 5.4), and were reflected in the ordination plot with a common trajectory of increasing development for the four main species (Figure 5.5). However, there was no significant difference among species or stages (MRPP: species P > 0.05, A = 0.078; stage P > 0.05, A = 0.191), nor were there any other obvious groups which were formed in the ordination. In general, newly hatched protolarval carp, Australian smelt and rainbowfish, all fed predominantly on rotifers, copepod nauplii or algae (Table 5.4). As the larvae grew, they broadened their diets to feed on a range of microfauna (typically chydorids, rotifers, macrothricids and cyclopoids) and small macroinvertebrates (typically chironomid larvae and pupae). As juvenile/adults, rainbowfish and Australian

Table 5.4: Dietary composition by percent volume for each developmental stage of carp, Australian smelt, gambusia, rainbowfish, carp gudgeons and Murray cod. Only the first ten dominant (by volume) dietary items are shown. For full list see Appendix B. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL = postlarvae, PL1 = postlarvae 1, PL2 = postlarvae 2.

Species		Carp				Australian smelt				Gambusia			Rainbowfish				Carp gudgeons				Murray cod
Developmental stage		PR	PF	M	J	PR	PF	M	JA	PL1	PL2	JA	PR	PF	M	JA	PR	PF	M	JA	PL
No. fish analysed		21	60	30	41	73	28	60	123	54	127	201	83	95	127	142	8	5	4	59	73
P. Rotifera		2.38				37.49	35.32	8.34		8.61	4.36		24.17	21.73	8.32				16.53		
P. Nematoda									1.88												
P. Arthropoda																					
C. Crustacea																					
sub O. Cladocera																					
	F. Bosminidae						1.99														
	F. Chydoridae	10.58	27.55	16.72	11.95		8.16	9.06	1.41	10.05	14.13	5.36	0.55	2.15	5.21					9.40	8.45
	F. Daphniidae		7.90							5.16	2.62	3.43								2.39	
	F. Ilyocryptidae				1.35								0.40	4.73	6.75						2.49
	F. Macrothricidae		3.11	3.00	11.39	0.91	11.17	7.59		8.15	8.78	3.43	1.23	9.84	19.48	3.00					29.66
	F. Moinidae						1.79														
	F. Sididae	4.76		3.87						1.79											
sub C. Ostracoda			1.36	2.89	5.96															1.82	
sub C. Copepoda																					
nauplii						12.47	10.54	2.51					1.88				94.58	2.00	51.62	3.67	
Cyclopoida			26.93	18.17	5.41	2.28	8.11	7.72		28.49	28.49	7.13		2.18	3.54				25.49	19.80	17.31
Harpacticoida			1.25					3.18					0.27	3.09							
C. Collembola														2.17	3.66	2.93					
C. Insecta																					
O. Ephemeroptera									2.90			3.42				1.91					2.28
O. Hemiptera	F. Corixidae				24.16				1.08		3.25	14.67				13.32					
O. Coleoptera (Adult)									1.73							2.65					
O. Diptera	F. Chironomidae		16.41	39.32	22.46		1.10	10.21	11.79	2.23	7.62	9.59	0.51	2.49	3.71	4.75				3.13	8.63
	F. Chironomidae pupae			2.85	1.42			3.97	52.34		7.38	20.53				13.83				27.73	6.46
	F. Simulidae																				1.68
	F. Tipulidae			1.67	2.48																
O. Trichoptera									1.06												
Algae		35.32	1.23			5.71	4.17						32.01	14.67	6.68	1.94					
Terrestrial invertebrate								12.36	13.22	1.76	4.88	13.72			5.79	32.50				3.08	
Invertebrate egg			2.89	2.75						1.77											
Sand grains		4.76				8.61							0.45								6.39
Unidentified matter		42.20	7.01	5.50	7.35	32.53	13.45	20.01	6.82	24.99	9.79	8.79	37.89	34.05	18.98	8.85	5.42	2.00	4.36	9.08	15.00

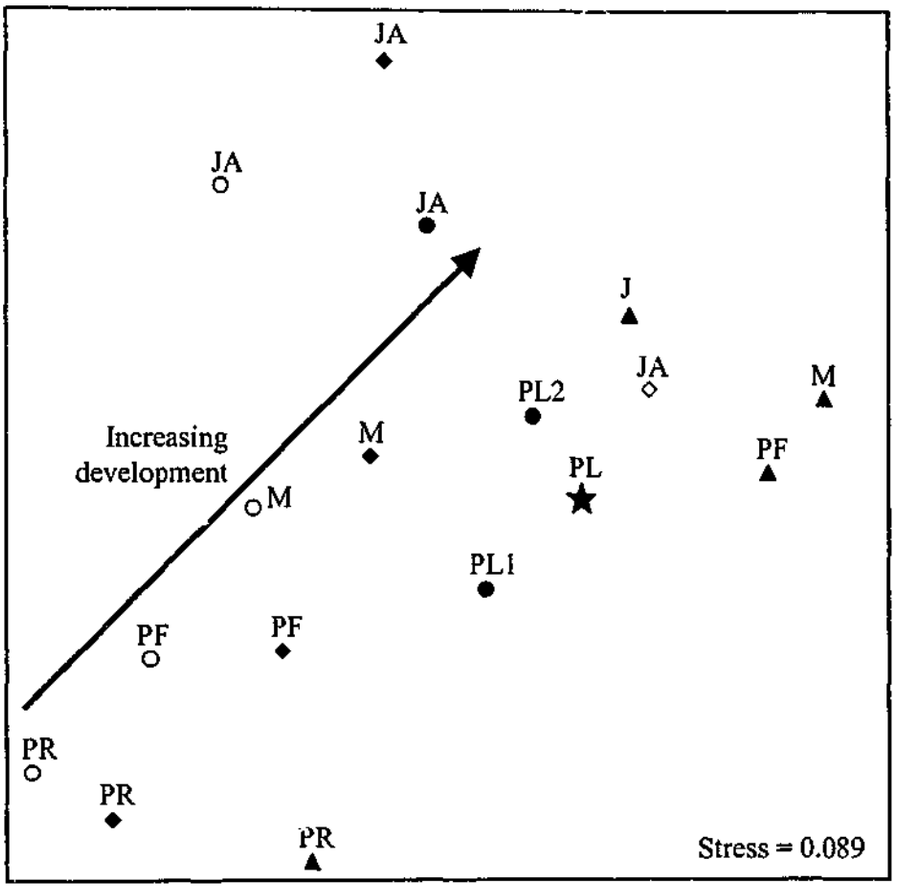


Figure 5.5: Two-dimensional solution for NMDS of volumetric dietary data for developmental stages for ◆ carp, ▲ Australian smelt, ● gambusia, ○ rainbowfish, ◇ carp gudgeons and ★ Murray cod. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2, PL = postlarvae. (30 random starts, maximum of 200 iterations, minimum stress = 0.089). Arrow indicates direction of increasing development.

smelt consumed mainly terrestrial invertebrates, chironomid pupae and larvae, whereas juvenile carp ate predominantly chironomid larvae and corixids. Gambusia postlarvae fed mainly on cyclopoids and chydorids and switched to chironomid pupae, corixids and terrestrial invertebrates as juvenile/adults. Carp gudgeon larvae consumed mostly copepod nauplii, whilst juvenile/adults ate chironomid pupae and cyclopoids. Murray cod postlarvae ate predominantly macrothricids and cyclopoids.

Some prey taxa are known to be associated with specific zones in the water column (eg. pelagic or epibenthic) and from this the area where individual fish had been feeding prior to capture was estimated. As they developed, carp, Australian smelt, gambusia and rainbowfish appeared to change their feeding zones (Figure 5.6). Carp showed a steady increase in their consumption of epibenthic prey through ontogeny (Figure 5.6a). Australian smelt as protolarvae ate predominantly pelagic prey items, such as rotifers and copepod nauplii, but consumed relatively more epibenthic prey as they developed through the larval stages (Figure 5.6b, Table 5.4). However, the diet of juvenile/adult Australian smelt consisted of a smaller proportion of pelagic prey than for larvae, and increased their consumption of epibenthic/pelagic prey, such as chironomid pupae. Epibenthic prey comprised similar proportions of the diet of gambusia throughout ontogeny (Figure 5.6c). However, the amount of pelagic prey consumed decreased through ontogeny, with juvenile/adult gambusia consuming more surface and epibenthic/pelagic prey items (Figure 5.6c). The diet of protolarval rainbowfish consisted predominantly of pelagic and epibenthic/pelagic prey, however they decreased in contribution to the diet throughout the larval stages, with relatively more epibenthic prey consumed (Figure 5.6d). Juvenile/adult rainbowfish consumed similar proportions of epibenthic, surface and epibenthic/pelagic prey. Both juvenile/adult carp gudgeons and Murray cod postlarvae consumed mostly epibenthic prey (Figure 5.6c & f).

Dietary breadth values for each species and developmental stage were high compared with other studies (Scrimgeour and Winterbourn 1987, Pen *et al.* 1993, Hyndes *et al.* 1997), with Murray cod postlarvae displaying the widest dietary breadth (Figure 5.7). Dietary breadth remained similar throughout ontogeny for both carp and gambusia. The dietary breadth of rainbowfish increased throughout the larval stages and decreased slightly as juvenile/adults. The dietary breadth of Australian smelt was consistent throughout their larval stages but decreased sharply as juvenile/adults.

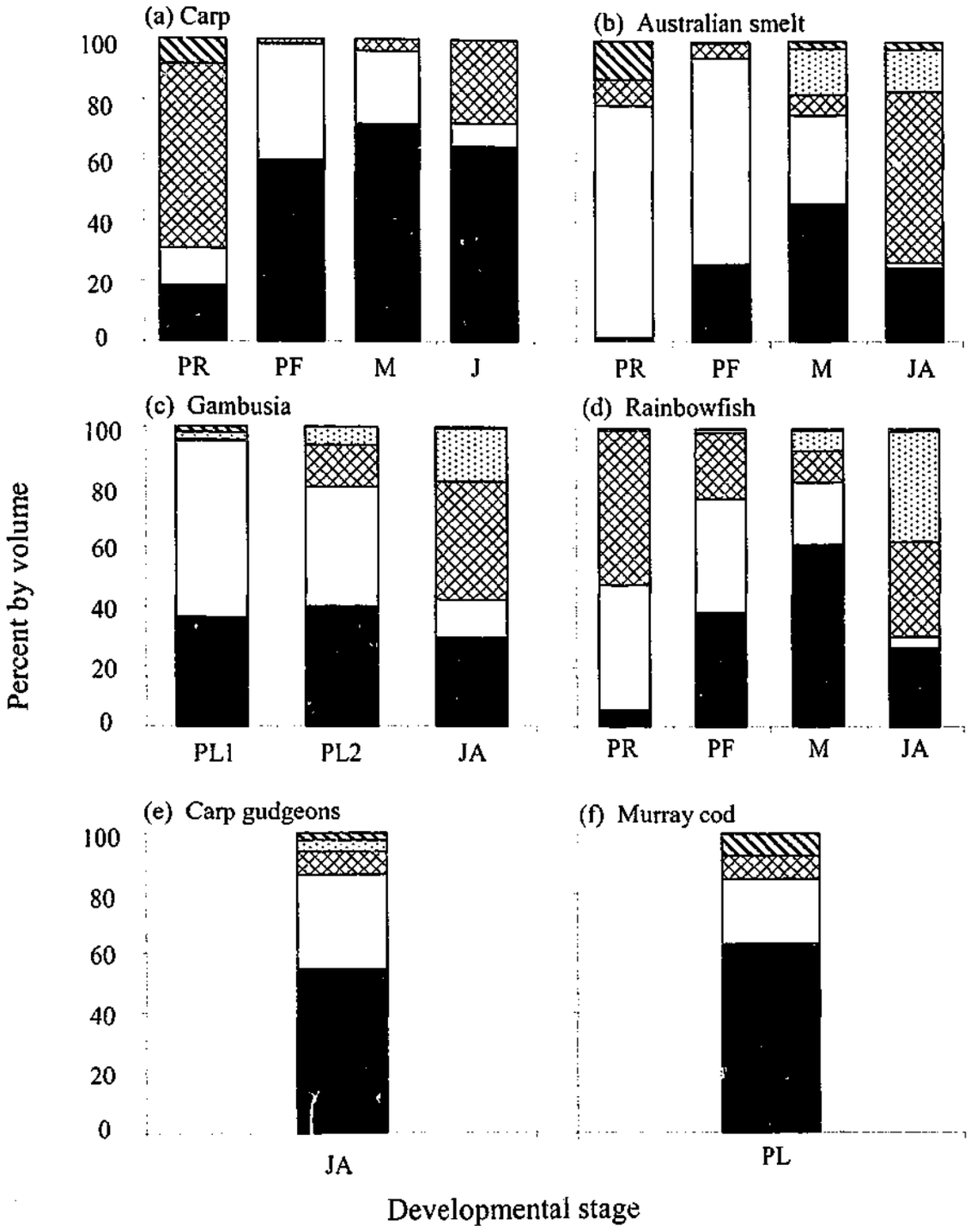


Figure 5.6: Percent by volume of prey in different habitat zones, for each developmental stage of (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish, (e) carp gudgeons and (f) Murray cod. Habitat zones: ■ epibenthic, □ pelagic, ⊠ epibenthic/pelagic, ⊡ surface, and ▨ other. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2, PL = postlarvae.

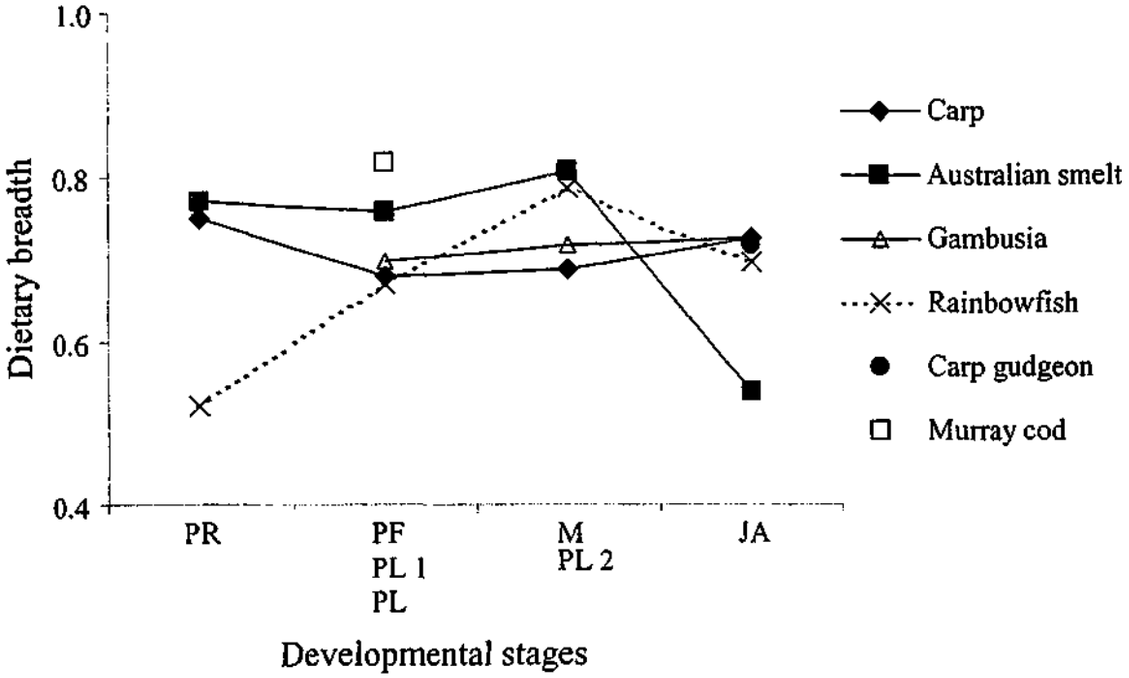


Figure 5.7: Dietary breadth values for each developmental stage of each species. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, JA = juvenile/adult, PL = postlarvae, PL1 = postlarvae 1, PL2 = postlarvae 2.

Dietary overlaps

Overlap values between species and stages were generally low, with only a few considered biologically significant (Table 5.5). Furthermore, most biologically significant values were relatively low (all were < 0.80) and were commonly between sequential developmental stages of the same species. One of the highest interspecific overlaps that occurred was between protolarval rainbowfish and protolarval carp. However, the larval stages of the two species do not overlap in time (see Chapter 4) and therefore there is no chance for competition for food resources.

In general, the diets through ontogeny of the species that occurred in the same habitats and at the same time, were significantly different from each other in both cases (MRPP: carp / Australian smelt $P < 0.001$, $A = 0.077$; gambusia / rainbowfish $P < 0.0001$, $A = 0.126$, Figure 5.8). This was true for interspecific comparisons of most developmental stages and mouth gape size, however, intraspecific overlaps did occur between larval stages of Australian smelt, gambusia and rainbowfish, but not for carp (Table 5.6). The diets of protolarval carp and Australian smelt were marginally similar (MRPP: $P > 0.05$, $A = 0.194$, Figure 5.8a, Table 5.6), with both species at the protolarval stage consuming algae. However, their diets became significantly different from each other through ontogeny. Interestingly, although juvenile/adult gambusia and rainbowfish showed similar diets over all the habitats sampled (Table 5.4 and 5.5), their diets did not significantly overlap in backwaters and still littoral habitats (Figure 5.8b, Table 5.6), as gambusia ingested predominantly chironomid larvae and cyclopoids, while rainbowfish consumed mainly terrestrial invertebrates.

Table 5.5: Dietary overlap values (Schoener's index) and mean (1 SE) gape size between all stages and species of fish. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL = postlarvae, PL1 = postlarvae 1, PL2 = postlarvae 2. Values above 0.60 are shown in bold and are considered to be biologically significant (Zaret and Rand 1971, Mathur 1977, Wallace 1981).

			Carp				Australian smelt				Gambusia			Rainbowfish				Carp gudgeon
	Stage	Mean gape (mm)	PR	PF	M	J	PR	PF	M	JA	PL1	PL2	JA	PR	PF	M	JA	JA
Carp	PR	0.42 (0.01)																
	PF	0.79 (0.02)	0.37															
	M	1.17 (0.02)	0.38	**0.67**														
	J	2.43 (0.19)	0.36	0.49	0.59													
Australian smelt	PR	0.27 (0.01)	0.50	0.24	0.22	0.23												
	PF	0.50 (0.01)	0.44	0.34	0.32	0.38	**0.77**											
	M	0.76 (0.02)	0.45	0.51	0.50	0.52	0.42	0.58										
	JA	1.57 (0.05)	0.26	0.25	0.26	0.29	0.21	0.15	0.49									
Gambusia	PL1	0.66 (0.01)	0.49	**0.69**	0.54	0.48	0.38	0.57	**0.67**	0.27								
	PL2	0.99 (0.01)	0.40	**0.66**	0.57	0.51	0.29	0.45	**0.66**	0.36	**0.79**							
	JA	1.73 (0.03)	0.32	0.40	0.39	0.53	0.24	0.30	**0.63**	**0.62**	0.44	0.56						
Rainbowfish	PR	0.31 (0.01)	**0.75**	0.27	0.25	0.26	**0.69**	0.59	0.44	0.25	0.44	0.32	0.27					
	PF	0.43 (0.01)	0.57	0.35	0.31	0.41	**0.64**	**0.67**	0.58	0.29	0.57	0.47	0.36	**0.76**				
	M	0.65 (0.02)	0.46	0.38	0.35	0.46	0.44	0.54	**0.70**	0.32	0.59	0.55	0.45	0.48	**0.71**			
	JA	1.98 (0.07)	0.31	0.24	0.24	0.39	0.27	0.23	0.50	0.51	0.39	0.43	**0.68**	0.31	0.39	0.43		
Carp gudgeon	JA	2.00 (0.10)	0.38	**0.63**	**0.70**	**0.61**	0.30	0.38	0.59	0.34	**0.61**	**0.62**	0.51	0.31	0.37	0.44	0.36	
Murray cod	PL	1.24 (0.01)	0.42	0.51	0.53	0.50	0.33	0.45	0.58	0.32	0.59	**0.63**	0.47	0.30	0.45	0.55	0.32	0.57

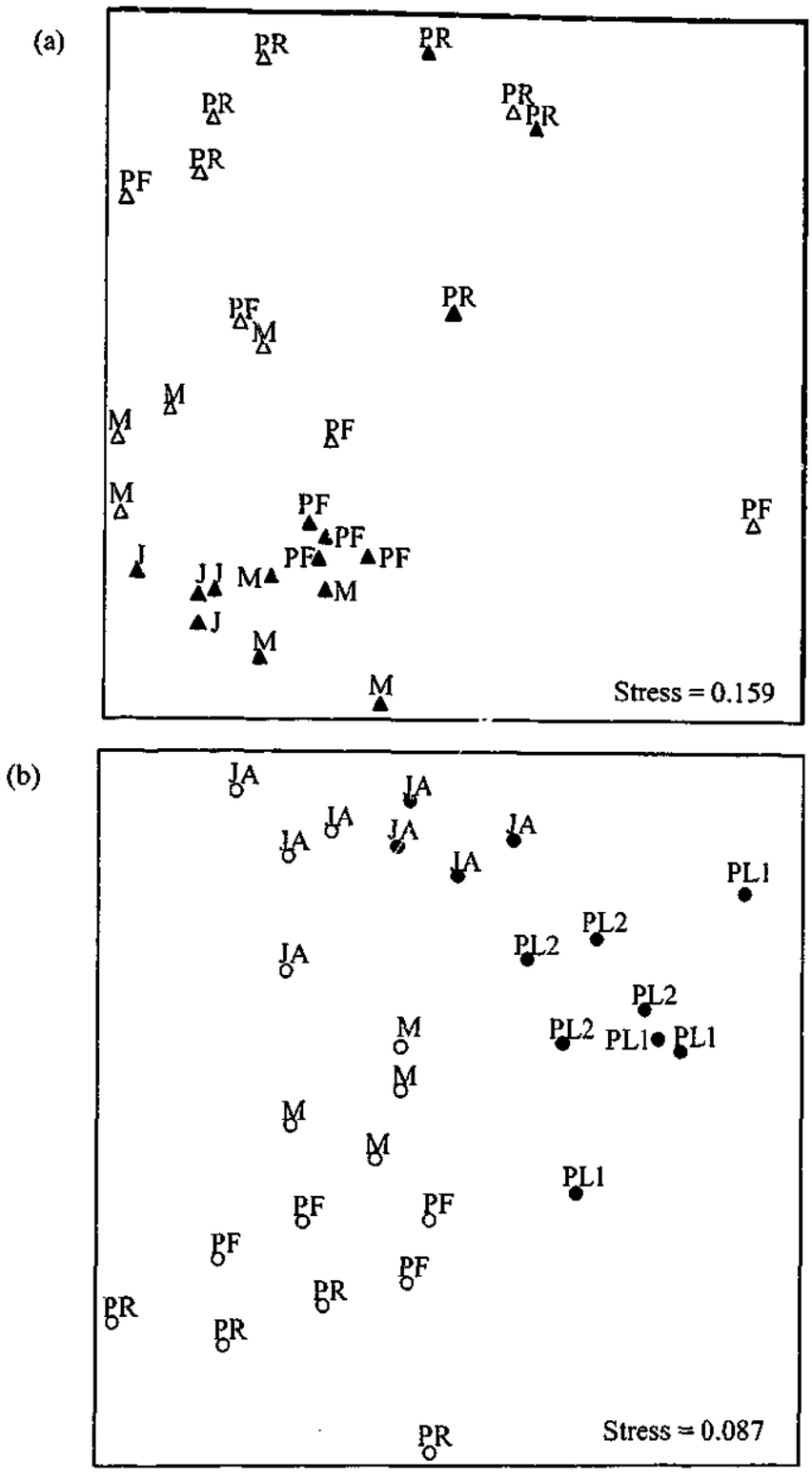


Figure 5.8: Two-dimensional solution of NMDS of volumetric data to examine dietary overlaps for all developmental stages of (a) ▲ carp and △ Australian smelt, and (b) ● gambusia and ○ rainbowfish, which occur in the same habitats (backwaters and still littorals) at the same time. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2. (30 random starts, maximum of 200 iterations).

Table 5.6: Significance values of difference between groups using MRPP analysis for diets of species occurring in the same habitats (backwaters and still littorals) at the same time for all developmental stages of Australian smelt and carp, and rainbowfish and gambusia. Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, J = juvenile, JA = juvenile/adult, PL = postlarvae, PL1 = postlarvae 1, PL2 = postlarvae 2. Values where P > 0.05 are considered non significant (ie. no difference between diets and therefore their diets overlap) are shown in bold.

		Australian smelt			Carp			
		PR	PF	M	PR	PF	M	J
Mean gape (1 SE) (mm)		0.42 (0.01)	0.27 (0.01)	0.50 (0.01)	0.76 (0.02)	0.79 (0.02)	1.17 (0.02)	2.43 (0.19)
Australian smelt	PF	**0.099**						
	M	0.011	**0.750**					
Carp	PR	**0.064**	0.008	0.006				
	PF	0.007	0.008	0.006	0.005			
	M	0.008	0.017	0.007	0.005	0.045		
	J	0.007	0.007	0.008	0.005	0.006	0.009	

		Gambusia			Rainbowfish			
		PL1	PL2	JA	PR	PF	M	JA
Mean gape (1 SE) (mm)		0.42 (0.01)	0.66 (0.01)	0.99 (0.01)	0.31 (0.01)	0.43 (0.01)	0.65 (0.02)	1.98 (0.07)
Gambusia	PL2	**0.561**	-					
	JA	0.006	0.006	-				
Rainbowfish	PR	0.008	0.006	0.006	-			
	PF	0.007	0.005	0.005	**0.394**	-		
	M	0.006	0.006	0.006	0.005	0.024	-	
	J	0.006	0.006	0.012	0.006	0.006	0.007	-

5.4 Discussion

Flexible 'critical' first feeding period and the importance of size

The critical first feeding period, when young fish have absorbed all of their yolk sac and start exogenous feeding (Hjort 1914, May 1974), is thought to mark the greatest level of natural mortality in a fish's life. In the present study, a large proportion of first feeding larvae of three species, Murray cod, Australian smelt and carp, were all found to be able to feed externally before their yolk sac was completely absorbed. A similar finding was also observed by Mann *et al.* (1997) in the River Great Ouse, where a small number of first feeding roach larvae also had partial yolk sacs present. The flexibility generated by having a transitional overlapping period of both exogenous and endogenous feeding could allow larvae to develop their feeding skills and to overcome patchy distributions of their prey (Balon 1986).

Since fish larvae are gape-limited predators, gape size can influence the composition of the diet, with the mean prey size increasing as the mouth gape and length of the fish increases (Wong and Ward 1972, Schael *et al.* 1991, Bremigan and Stein 1994). In the present study, gape size was generally a good predictor of the size of the maximum prey item in the gut, but was rarely a good predictor of the minimum size of prey items. Carp, Australian smelt, gambusia and rainbowfish all consumed prey as big as their mouth gape, but also selected a range of smaller prey items. A similar pattern has also been observed in other studies (Mark *et al.* 1987, Schael *et al.* 1991, Bremigan and Stein 1994). Schael *et al.* (1991) demonstrated that the maximum prey size of larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*) and black crappie (*Pomoxis nigromaculatus*) all increased with increasing mouth gape, but that all three species still consumed large numbers of prey substantially smaller than their mouth gape. However, Murray cod and to a lesser extent carp gudgeons, did not consume prey up to their maximum mouth gape size. Indeed, over the small size range (7.8 – 10.0 mm) of Murray cod examined in this study, there was no relationship between gape size and either the size of the largest or smallest prey. Additionally, Murray cod consumed prey items considerably smaller than their mouth gape.

Miller *et al.* (1988) investigated the relationship between size at hatching and a number of key early life history features. They suggested that large larvae at hatching are capable of feeding earlier, have a longer period before irreversible starvation or 'the point of no

return' and take longer to absorb their yolk sacs. Larger fish can also generally swim faster (Blaxter 1986, Miller *et al.* 1988), have better vision (Blaxter 1986), and are likely to be less vulnerable to predation (Miller *et al.* 1988). The life-history strategy of producing a small number of large larvae may also be advantageous in prey-poor environments (Winemiller and Rose 1993).

At first feeding, Murray cod are well developed, with a large body size and large mouth gape, and are also able to consume relatively large prey items, such as cyclopoids, chydorids and macrothricids, compared to other first feeding larvae. Murray cod are likely therefore, to be highly flexible in the timing of their first feed, to be less at risk of starvation and are also able to consume a wide variety of prey types at first feeding. These factors combined, suggest that Murray cod are well adapted to the vagaries of finding patchy food resources in the main channel environment and may therefore not need to rely on high densities of prey that may occur only on the inundated flood plain.

Dietary composition and ontogenetic diet shifts

Most native fish in the Murray-Darling Basin are opportunistic carnivores, consuming mainly macro- and microinvertebrates (McDowall 1996, Kennard *et al.* 2001, Schiller and Harris 2001). This broad feeding strategy has been shown to exist for the majority of developmental stages of the species examined in this study. However, protolarval rainbowfish and carp are notable exceptions, being omnivorous and consuming large amounts of algae.

Four species in the present study, carp, Australian smelt, gambusia and rainbowfish were shown to exhibit significant ontogenetic dietary shifts. Although only postlarval Murray cod were examined in this study, adult cod are known to consume mainly fish and large crustaceans such as shrimp and crayfish (Harris and Rowland 1996), demonstrating a significant ontogenetic dietary change in this species. Major ontogenetic dietary changes can occur with either a concurrent change in habitat use or within the same habitat type (Osenberg *et al.* 1994). Of the five species in this study, carp, Australian smelt and Murray cod exhibited significant concurrent changes in diet and habitat (Figure 5.9 a, b & e). Additionally, carp showed another significant change in diet at the postflexion and metalarval stage. The intermediate metalarval developmental stage was often a transitional

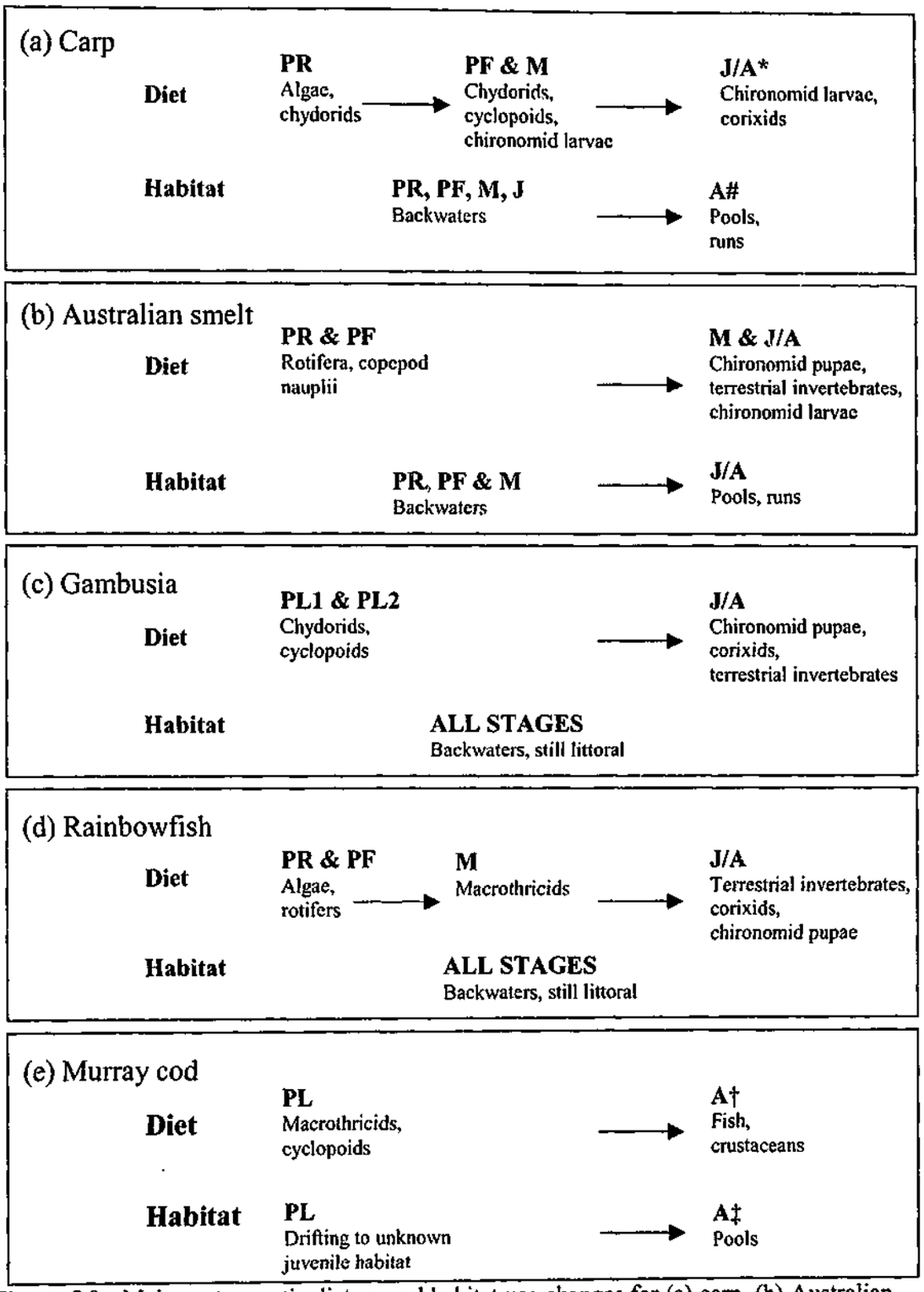


Figure 5.9: Major ontogenetic dietary and habitat use changes for (a) carp, (b) Australian smelt, (c) gambusia, (d) rainbowfish and (e) Murray cod. Habitat use data from Chapter 4. * = Adult carp diet (Hume *et al.* 1983), # = Adult carp habitat (Crook *et al.* 2001), † = Adult Murray cod diet (McDowall 1996), ‡ = Adult Murray cod habitat (Koehn 1997). Developmental stages: PR = protolarvae, PF = postflexion, M = metalarvae, JA = juvenile/adult, PL1 = postlarvae 1, PL2 = postlarvae 2, PL = postlarvae.

stage in the diet of a number of species, where individuals consumed both typical early larval and juvenile/adult prey items. Whilst rainbowfish and gambusia did not alter their habitat use through ontogeny, their diet did significantly change with development (Figure 5.9 c & d).

Only two other studies have examined the diets of larval freshwater fish in natural systems in Australia. Gehrke (1992) found that small (< 5 mm) carp gudgeons in a billabong consumed mainly rotifers, before switching to copepods and cladocerans as larger larvae. The present study did not capture sufficient numbers of carp gudgeons to allow for a definitive comparison. However, from the few individuals that were examined, protolarval carp gudgeons (< 5 mm) ate only copepod nauplii, while older larvae consumed rotifers, copepod nauplii and cyclopoids. Villizzi (1998) examined the ontogenetic dietary pattern of carp in the lower Murray River. He found that carp ate predominantly cladocerans (mainly *Daphnia sp.*) throughout all larval stages and acquired a more benthic feeding behaviour as juveniles. In the present study, carp larvae began feeding on algae and chydorids, but consumed more epibenthic prey, such as chironomid larvae and chydorids, as the larvae developed into juveniles; thus supporting Villizzi's (1998) observed switch to more benthic feeding as juveniles. The diet observed for postlarval Murray cod in the present study, consisting mainly of cyclopoids and cladocerans, generally corresponds to previous studies on their diets in aquaculture ponds (Lake 1967b, Rowland 1992). However, in aquaculture systems, Murray cod postlarvae mostly consumed daphniids and moinids, whereas in the wild they preferred more benthic-orientated cladocerans such as macrothricids and chydorids.

The species and developmental stages examined in this study obtained food from a range of feeding zones in the water column, including the water surface, epibenthic and pelagic zones. Whilst pelagic zone microfauna and flora such as algae, rotifers and copepod nauplii were important in the diets of a number of species at the early larval stages, epibenthic and surface dwelling fauna generally became more important through ontogeny. However, first feeding Murray cod consumed a large proportion of epibenthic prey, relative to other prey zones, confirming aquarium observations that they feed predominantly in the epibenthic zone (pers. obs).

Juvenile/adults of rainbowfish, Australian smelt and gambusia consumed large numbers of terrestrial invertebrates that accidentally fell or landed on the water surface. Terrestrial invertebrates, including insects of the orders Hymenoptera, Hemiptera and Coleoptera and Arachnids are often reported to be an important food resource for fish in freshwater systems (eg. Cadwallader *et al.* 1980, Garman 1991, Edwards and Huryn 1996, Nakano *et al.* 1999). Adult gambusia have been reported previously to consume a large variety of terrestrial invertebrates (Arthington 1989, Pen and Potter 1991, Pen *et al.* 1993, García-Berthou 1999). For example, gambusia in subtropical streams in southern Queensland, mainly consumed prey of terrestrial origin, such as Hymenoptera and adult Diptera (Arthington 1989). Lieschke and Closs (1999) examined the diet of adult Australian smelt in a Murray River billabong, and found their diets to be dominated by cladocerans. However, in the present study, Australian smelt changed their diets from predominantly pelagic feeding as larvae to probably surface feeding as adults, consuming chironomid pupae and terrestrial invertebrates. Whether Australian smelt consistently has different diets in rivers than billabongs requires further investigation.

Partitioning of food resources throughout ontogeny

For all the species and developmental stages examined in the present study, surprisingly only a few minor dietary overlaps occurred. Moreover, the higher overlaps were commonly between sequential stages of the same species, reflecting subtle ontogenetic changes in diet. This contrasts with the results of other studies on dietary overlaps through ontogeny of closely related species, that have found greater interspecific than intraspecific overlaps (Mol 1995, Garner 1996). Mol (1995), in a study on the ontogenetic dietary overlaps of three closely related neotropical armoured catfishes (*Hoplosternum spp.*), found large overlaps in the diet among larvae, juvenile and adults of all three species, but considerably lower intraspecific overlaps within the three species. However, all the species examined in the present study are taxonomically distant from each other, with two of the species, carp and gambusia, introduced into Australia. Therefore they are likely to exhibit major morphological, behavioural and ecological differences from each other, and this is likely to have contributed to their relatively separate feeding preferences demonstrated in this study.

Competition for resources between newly introduced and native species is thought to be common, although it is very difficult to demonstrate (Li and Moyle 1993). In Australia,

both carp and gambusia are widely speculated to prey on, and have similar diets to, native species (Cadwallader 1978, Arthington *et al.* 1983, Hume *et al.* 1983, Lloyd 1987, Arthington 1989, Koehn *et al.* 2000). Gambusia is a generalist carnivore, and is likely to be flexible in its dietary preferences (Arthington 1989, Pen and Potter 1991). It has been speculated to have considerable overlap with several families of Murray-Darling fishes (Lloyd 1987, Arthington and Lloyd 1989) and has been implicated in the decline of a number of small native species (Arthington *et al.* 1983, Lloyd and Walker 1986). Pen and Potter (1991) and Pen *et al.* (1993), in dietary studies of adult gambusia and small native fish in the south-western region of Western Australia, found no evidence of dietary overlap with a number of small native species. In the present study, gambusia were also found not to exhibit any biologically significant overlaps with any other species. This is despite gambusia and rainbowfish having similar mouth morphologies, size, schooling behaviour and habitat use.

Hume *et al.* (1983) suggested that dietary overlaps might occur between adult carp and Australian smelt, western carp gudgeons and flat-headed galaxiids. In addition, there has been much speculation as to the degree of overlap in the diets of young carp and young native species (Koehn *et al.* 2000). The present study found little evidence of any biologically significant overlap with larval and juvenile carp and other species. The highest dietary overlap was between protolarval carp and protolarval rainbowfish, however the larval stages of these two species do not occur at the same time, and therefore competition for food resources is unlikely. Larvae of Australian smelt and carp do occur at the same time, however, their diets were significantly different overall and were only marginally similar in their main nursery habitats.

Ontogenetic resource shifts can potentially complicate community interactions such as competition (Werner and Hall 1979, Werner and Gilliam 1984). Werner and Gilliam (1984) suggested that competition for food resources between species may be more pronounced at the early life stages than as adults, and that these "juvenile bottlenecks" may influence future recruitment strength of a species. Since most fish larvae are thought to require small prey items at first feeding, major dietary overlaps between species at the early developmental stages are likely. Indeed some studies have demonstrated that high dietary overlaps occur during the early larval period of co-occurring species, while as juveniles and adults the species' dietary preferences diverge and became more specialised

(Mark *et al.* 1987, Perrson and Greenberg 1990, Garner 1996). For example, Garner (1996) found that the early larval stages of five species of cyprinids in the River Great Ouse fed predominantly on rotifers and diatoms, and then switched to cladocerans during the late larval period. However, as juveniles, the five species diverged and established species-specific dietary selection.

In the previous chapter, it was demonstrated that Australian smelt larvae shared backwater and still littoral nursery habitats with larval and juvenile carp, while later in the summer all developmental stages of rainbowfish and gambusia shared backwaters and still littoral habitats. It was therefore hypothesised, that this co-occurrence may also give rise to significant dietary overlap and competition, especially at the first feeding larval stages. However, for both co-occurrences, each species generally differed in its dietary preference through ontogeny and did not significantly overlap with the dietary preferences of any developmental stage of the other species. The only exception was a minor overlap in the diets of protolarval Australian smelt and carp. However, it must be stressed that both co-occurrences involved introduced species, and therefore the dietary preferences of the native species may be altered from natural conditions. Further research is required into the diets of these species in both allopatric and sympatric conditions to determine whether the lack of overlap is due to inherent behaviours or competitive interactions between the species.

Concluding remarks

The 'flood recruitment model' (FRM) proposes that larvae of all native species in the Murray-Darling Basin require dense blooms of small zooplankton such as rotifers and small crustaceans, to sustain them through the larval stages (Arumugam and Geddes 1987, Harris and Gehrke 1994). In this chapter, it was established that not all first feeding larvae require small prey, and those that do, soon alter their diets to feed on a variety of larger prey items. There was also little evidence of prey specialisation, with most developmental stages and species consuming a variety of prey from epibenthic, pelagic and surface feeding zones. In the next chapter, I characterise the types and quantities of prey items available in the main channel environment, without inputs from the inundated floodplain.

Chapter 6: Density and Distribution of Potential Prey for Larval and Juvenile Fish within the Main Channel: the Role of Pelagic and Epibenthic Meiofauna

6.1 Introduction

The first exogenous feeding period is believed to be critical to the early life stages of fish, because larvae that fail to feed sufficiently may die due to starvation, or may grow relatively slowly, increasing their risk of predatory mortality, compared to well fed, fit individuals (May 1974, Houde 1997). The match/mismatch hypothesis proposes that the supply of adequate densities of food to all larval stages, controls the strength of larval survival and subsequent recruitment (Cushing 1990). The hypothesis suggests that for strong recruitment to occur, the peak production of both fish larvae and their prey need to overlap (Cushing 1990). The densities of prey required for the survival of larvae have been variously proposed as between 100 and 1000 individual prey items L^{-1} (May 1974, Gerking 1994, Bone *et al.* 1995). In the rearing of Australian native freshwater fish in aquaculture environments, 500 individuals L^{-1} is commonly used as a critical density of prey items before larvae are stocked into the rearing ponds (Ingram, B., Marine and Freshwater Resources Institute, Victoria, pers. comm.). Rowland (1992) found that changing the densities of zooplankton between 250 – 5000 L^{-1} did not affect the survival rates of hatchery-reared Murray cod larvae, although if the initial feeding period was delayed, survival was significantly lower at 250 than at 3000 zooplankters L^{-1}.

There are currently two hypotheses that speculate as to the source of high densities of prey that can sustain successful fish recruitment in floodplain rivers of the Murray-Darling Basin. The 'flood recruitment model' (FRM), which is predominantly derived from the flood pulse concept (Junk *et al.* 1989), proposes that flooding enhances recruitment by providing access to abundant food and habitat on the inundated flood plain (Harris and Gehrke 1994, Schiller and Harris 2001). This hypothesis stems from the assumption that the main channel environment does not support high enough densities of adequately sized zooplankton to sustain larval fish (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992). Flooding may also indirectly enhance recruitment in the main channel, through the production of nutrients, organic matter and potential prey on the inundated flood plain, which is then transported in returning waters to

the main channel (Junk *et al.* 1989). In comparison, the 'low flow recruitment hypothesis' (LFRH) (Humphries *et al.* 1999), suggests that some fish species are able to spawn and successfully recruit during the summer low flow period, due to an increase in the concentrations of prey for fish larvae during low flow periods.

The previous chapter demonstrated that not all fish larvae require small prey at first feeding, and those that do, soon alter their diets as older and larger larvae to consume a wide variety of larger prey items. Meiofauna are those animals intermediate in size between true macro- and microfauna; or those that pass through 1000 µm but are retained on 63 µm sieves (Robertson *et al.* 2000a). Lotic meiofauna will therefore include microcrustaceans and rotifers, which remain in this size category throughout all of their life cycle; but also include the early developmental stages of many macroinvertebrate taxa such as chironomids and trichopterans (Robertson *et al.* 2000a). Meiofauna are abundant and diverse in riverine environments, and are speculated to play a range of ecological roles (Robertson 2000, Schmid-Araya and Schmid 2000, Hakenkamp and Morin 2000). Lotic meiofauna have potentially important functional roles in ecosystem processes, such as the mobilisation of organic matter, consumption of detritus, mineralisation of leaf material, and stimulating microbial production and metabolism (Hakenkamp and Morin 2000). Thus, meiofauna may contribute a significant component of total stream production and biomass (Robertson *et al.* 2000b). In addition, meiofauna act as an important trophic link between microbes and larger fauna such as macroinvertebrates and fish (Rundle and Hildrew 1992, Schmid-Araya and Schmid 2000, see Chapter 5).

Whilst a number of studies in Australia have established that high densities of meiofauna can occur in floodplain habitats during both high and low flow conditions (eg. Crome 1986, Crome and Carpenter 1988, Tan and Shiel 1993), only a few studies have examined densities within the main channel of lowland rivers (Shiel *et al.* 1982, Shiel 1985, Kobayashi *et al.* 1998). Shiel *et al.* (1982) and Shiel (1985) found low average densities of zooplankton (< 150 individuals L^{-1}) in the pelagic zone across a number of seasons in the Murray and Darling Rivers, whereas average densities up to 803 individuals L^{-1} occurred in the tidal Hawkesbury-Nepean River system (Kobayashi *et al.* 1998). In the main channel of rivers elsewhere, zooplankton biomass often peaks during low flow periods, due to the increased water residence time (Ferrari *et al.* 1989, Pace *et al.* 1992, Thorp *et al.* 1994, Basu and Pick 1996). Some studies have also suggested that increased residence

time may also allow greater densities of zooplankton to occur in non-flowing zones (such as backwaters, bays, eddies and pools) within the river (Thorp *et al.* 1994, Basu and Pick 1996, Reckendorfer *et al.* 1999, Reynolds 2000).

Non-flowing zones, particularly backwaters and still littoral habitats, are important nursery habitats for a number of species of Murray-Darling Basin fish (Chapter 4). One of the reasons commonly suggested for the strong nursery habitat association of fish larvae in rivers, is the higher abundance of potential prey items in these littoral habitats relative to other main channel habitat types (Thorp *et al.* 1994, Humphries *et al.* 1999). The LFRH proposes that the food resource in larval fish nursery habitats includes an abundant supply of epibenthic prey, such as benthic microcrustaceans, rotifers and first instar insect larvae (Humphries *et al.* 1999). As was demonstrated in the previous chapter, the diet of the larvae of several species in the main channel environment does include large proportions of epibenthic prey items from a number of taxa. However, epibenthic fauna are not sampled adequately using traditional zooplankton sampling techniques, and therefore, densities of potential prey items for fish larvae in the main channel environment may have been previously underestimated.

The aims of this chapter are to: (i) establish whether suitable densities of potential prey items are available within the main channel environment during flows confined to the main channel, (ii) establish whether there is a greater density of potential prey in epibenthic than in pelagic zones, (iii) establish which habitats provide the greatest density of potential prey, and (iv) determine whether these habitats are those preferentially used by fish larvae.

6.2 Materials and methods

Study site

The study was conducted in the lowland reaches of the Broken River in north-east Victoria, Australia (Figure 2.2). A general description of the river is given in section 2.2. Sampling was conducted at one site (36°27'20''S, 145°51'20''E; referred to as the "middle" site in Chapter 4), downstream of the township of Benalla (Figure 2.2). This site was situated on private land, was easily accessible by foot and contained a variety of habitat types. The length of the river sampled varied among sampling times, from one to three river km, and was dependent on the availability of uncommon habitats, such as backwaters within the reach.

Sampling trips

A total of four sampling trips were conducted at approximately monthly intervals: 3 November, 1 December, 30 December 1998 and 27 January 1999). On each occasion, the site was sampled once during the day and once during the following night. Water level was relatively stable and remained confined to the main channel of the river throughout the study period (Figure 2.4).

Sampling gear and design

Sampling was conducted during the day and night in a habitat-specific manner, with samples collected from six habitat types: backwaters, still, slow and medium flowing littoral habitats, pools and runs (see Figure 2.5). Backwater habitats, commonly termed inshore bays or embayments in European studies (Schiemer and Spindler 1989, Schiemer *et al.* 1991), were generally less than 10 m^2, were typically found at the downstream end of beaches, and were characterised by still, shallow water with narrow entrances. Still littoral habitats differed from backwaters, in that they had no restricted entry point, with the entrance as wide as the habitat itself. Pool habitats occurred in the middle of the channel with slow flowing deeper water. Run habitats also occurred in the middle of the channel but were shallower and faster flowing. Three random replicate examples of each habitat type were sampled during the day and the following night. Habitats were not disturbed between the collection of the day and night-time samples. Day samples were always taken between 1000 and 1400 h, and night samples between 2100 and 2400 h. The sampled habitats were chosen randomly from habitats previously categorised and sampled for larval and juvenile fish in the preceding week (see Chapter 4). Water velocity in still habitats

ranged from 0 to 0.02 ms^{-1} (mean ± SE = 0.02 ± 0.00), slow habitats from 0.07 to 0.22 ms^{-1} (0.16 ± 0.04) and medium habitats from 0.17 to 0.47 m s^{-1} (0.32 ± 0.04).

Two methods, an epibenthic corer and a modified Schindler trap (Schindler 1969) (Figure 6.1), were used to characterise the epibenthic and pelagic zone, respectively, in each habitat sampled. The pelagic zone was sampled using 2 x 4 L Schindler traps and the 8 L of water was then poured through a 63 µm mesh net. Each sample was then washed into a storage jar and preserved in 95% ethanol. The epibenthos was sampled using an epibenthic corer, which consisted of a 12 cm tall, 4.4 cm diameter PVC tube, with a circular plastic flange glued 1 cm from the bottom of the PVC tube (Figure 6.1b). This flange allowed a measured 1 cm of sediment and 11 cm of overlying water to be sampled. To take the sample, the epibenthic core was pushed into the sediment and then immediately sealed with a fitted plastic cap. A paint scraper, with a flexible rubber surface glued onto it (Figure 6.1c), was then slid under the corer and was used to lift the sample out of the water and into a nearby bucket. The rubber surface on the paint scraper helped create a seal. Due to the suspected variation in the density and diversity of microfauna within a habitat and the small area sampled by the epibenthic core, three randomly allocated epibenthic core samples were taken from each habitat and pooled, therefore sampling a volume of 0.55 L per habitat. Organic material (including live and dead material) was separated from the sand and clay by swirling and washing filtered water through the sand in the bucket and then washing out the organic material into a 63 µm mesh net. This was repeated several times, and both the organic material and the remaining sediment were finally preserved in 95% ethanol in separate storage jars.

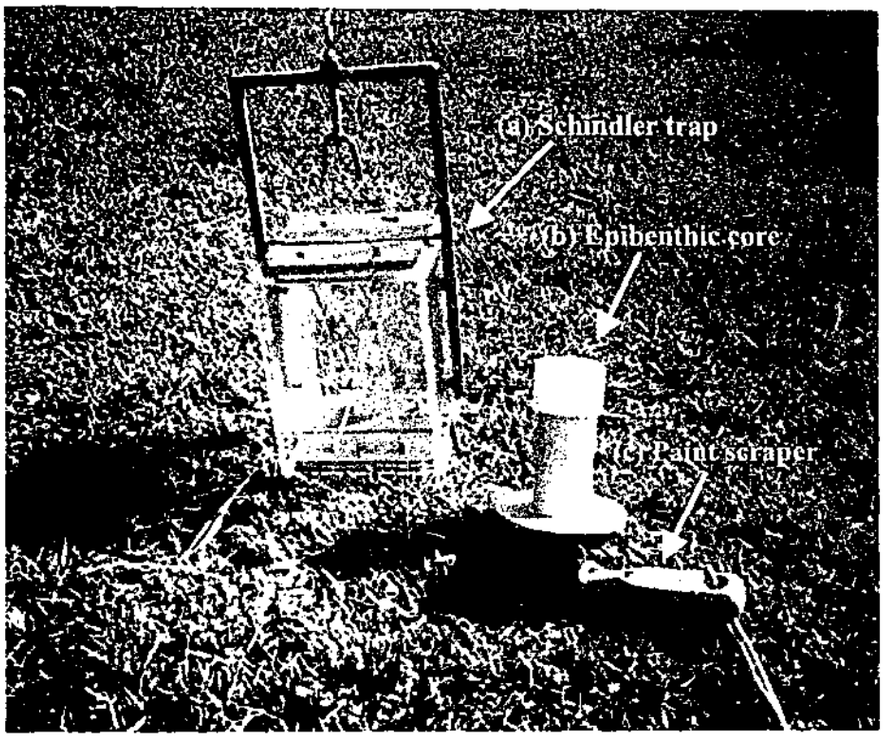


Figure 6.1: (a) Modified Schindler trap for sampling the pelagic zone, (b) core for sampling the epibenthic zone, and (c) a modified paint scraper used to lift the epibenthic core from the sediment.

Temperature and dissolved oxygen were measured with a Horiba U10 Water Quality Checker (Horiba Ltd, Japan) within each sampled habitat. Additionally turbidity, conductivity and pH were measured at three randomly selected sampling points at each site on each sampling trip, also using the Horiba Water Quality Checker. During the study period, water temperature ranged from 13.3 to 27.6 °C (mean ± SE = 22.29 ± 0.09), turbidity from 26 to 110 NTU (57.74 ± 2.40), conductivity from 90 to 250 $\mu S\ cm^{-1}$ (160 ± 10.00), pH from 6.60 to 7.83 (7.26 ± 0.04), and dissolved oxygen concentrations from 1.29 to 12.25 mg L^{-1} (7.40 ± 0.04). Temperature and dissolved oxygen varied significantly through time due mainly to seasonal variability, with water temperature generally increasing throughout the study period.

Laboratory processing

In the laboratory, each sample (whether an epibenthic or pelagic sample) was filtered through 63 µm mesh, transferred into a 100 mL beaker and the total volume of the sample made up to 50 mL. The sediment collected from epibenthic samples was again washed in small amounts using distilled water, with any remaining lighter organic material added to the 100 mL beaker. A number of the sediment samples were checked to establish whether any fauna still remained and no remaining fauna were found.

The 50 mL sample was stirred and 10 x 1 mL sub-samples were removed using a calibrated Gilson pipette. Each 1 mL sub-sample was examined in a Sedgewick Rafter counting cell, where all individuals were counted and identified, using a dissecting microscope with an inverted light source. All meiofauna were counted, including testate amoebae and small, first instar larvae of macroinvertebrates (eg. trichopterans and ephemeropterans), since they were considered small enough to be a potential food source for larval fish. Identifications were made using relevant taxonomic keys (Williams 1980, Shiel 1995, Hawking and Smith 1997), and by consulting with experts in the relevant taxonomic groups (R. Shiel and J. Hawking, Murray-Darling Freshwater Research Centre, pers. comm.).

Data analysis

All count data were converted to densities L^{-1}. The patterns in community composition for 'zone', 'trip', 'habitat' and 'day/night' were examined using non-metric multidimensional scaling (NMDS) in the software program PC-ORD™ (McCune and Mefford 1999). All

data were averaged between the three replicate habitats on each sampling trip. The first NMDS ordination included all data, and examined changes in community composition between the two sampling zones, epibenthic and pelagic. The two subsequent NMDS ordinations then assessed whether there were any patterns in the faunal composition in the epibenthic and pelagic zones separately. For all three ordinations, the averaged data were $\log_{10}(x+1)$ transformed and the Bray-Curtis similarity measure was used. The multi-response permutation procedure (MRPP) in PC-ORD™ (McCune and Mefford 1999), was used to establish whether there were significant differences in composition between sampling trip, habitat, and day/night, with the probability of achieving the result (P) and a descriptor of within-group homogeneity (A) reported. The Indicator Species Analysis tool in PC-ORD™ (McCune and Mefford 1999) was used to determine which species were the main contributors to the separation in the groups.

Separate 4-way analyses of variance (ANOVA's) with 'zone', 'trip', 'habitat' and 'day/night' as fixed factors, were used to apportion variance in the abundance of total fauna. Since testates contributed the greatest overall abundance in both epibenthic and pelagic zones, but were rarely eaten by larval and juvenile fish (see Chapter 5), ANOVA was conducted on both the total fauna and the total fauna excluding testates. Four-way ANOVA's were also conducted on the abundance of Rotifera, Chydoridae, Macrothricidae, Cyclopoida, copepod nauplii and Chironomidae, the main prey items for larval and juvenile fish (see Chapter 5). All data prior to analysis were checked to meet the assumptions of ANOVA by examining boxplots and plots of means versus variances and all data were subsequently $\log_{10}$ transformed prior to analysis. When ANOVA indicated a significant effect, *post hoc* comparisons were made using Tukey's test. All ANOVA's were performed using SYSTAT™ (Wilkinson 1990).

6.3 Results

Community composition

In total, 24 taxonomic groups were collected from the two zones (Table 6.1). Testate amoebae were the most abundant taxonomic group in both the epibenthic and pelagic zones, comprising 36% and 73% of the communities, respectively (Figure 6.2). Other major contributing taxa in the epibenthic zone were rotifers (5%), oligochaetes (4%) and ephemeropterans (4%) (Figure 6.2a). In the pelagic zone, other major taxa were rotifers (21%), copepod nauplii (12%), chydorids (7%) and oligochaetes (4%) (Figure 6.2b).

Table 6.1: Overall mean, standard error (SE), minimum and maximum density L^{-1} of each taxon, total fauna and total fauna excluding testates in the epibenthic and pelagic zones.

		Epibenthic				Pelagic			
Taxa		Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
P. Protozoa									
Testate amoebae		3812.75	377.68	54.81	25539.34	16.09	1.66	0.00	149.38
P. Rotifera		240.19	23.14	0.00	1625.89	9.39	1.05	0.00	66.25
P. Nematoda		15.13	2.33	0.00	164.42	0.07	0.02	0.00	1.88
P. Annelida									
C. Oligochaeta		209.31	16.90	0.00	968.23	2.03	0.33	0.00	27.50
P. Tardigrada		58.52	8.05	0.00	822.08	0.59	0.10	0.00	7.50
P. Arthropoda	F. Hydrachnidae	6.05	1.18	0.00	109.61	0.09	0.02	0.00	1.88
C. Crustacea									
sub O. Cladocera									
	F. Bosminidae	0.06	0.06	0.00	9.13	0.08	0.04	0.00	4.38
	F. Chydoridae	114.72	16.95	0.00	1415.81	3.38	0.81	0.00	80.00
	F. Daphniidae	1.08	0.42	0.00	36.54	0.39	0.16	0.00	16.88
	F. Ilyocryptidae	127.22	14.24	0.00	949.96	0.96	0.28	0.00	36.25
	F. Macrothricidae	84.33	11.94	0.00	1187.45	1.42	0.28	0.00	20.63
sub C. Ostracoda		14.63	2.02	0.00	118.75	0.17	0.03	0.00	3.13
sub C. Copepoda									
nauplii		50.68	7.17	0.00	602.86	5.46	2.67	0.00	336.25
O. Harpacticoida		41.37	4.44	0.00	274.03	0.42	0.14	0.00	18.75
O. Cyclopoida		44.21	7.37	0.00	694.20	1.04	0.29	0.00	28.75
O. Calanoida		0.13	0.09	0.00	9.13	0.11	0.04	0.00	5.00
C. Insecta									
O. Ephemeroptera		201.10	22.33	0.00	1361.00	0.82	0.15	0.00	16.25
O. Hemiptera	F. Corixidae	12.62	1.68	0.00	99.65	1.18	0.22	0.00	15.00
O. Diptera	F. Chironomidae	150.02	9.72	0.00	712.47	1.35	0.28	0.00	32.50
	F. Chironomidae pupae	1.14	0.28	0.00	18.27	0.03	0.01	0.00	1.25
	F. Simuliidae	0.32	0.14	0.00	9.13	0.02	0.01	0.00	1.25
O. Trichoptera		2.09	0.42	0.00	27.40	0.00	0.00	0.00	0.00
Terrestrial invertebrates		4.61	1.44	0.00	173.55	0.26	0.05	0.00	4.38
Unidentified material		11.52	1.65	0.00	109.61	0.07	0.02	0.00	2.50
TOTAL		5203.79	400.10	401.91	27572.12	45.43	4.45	4.38	430.00
TOTAL (excluding testates)		1391.04	60.05	255.76	4713.27	29.33	4.01	0.63	428.75

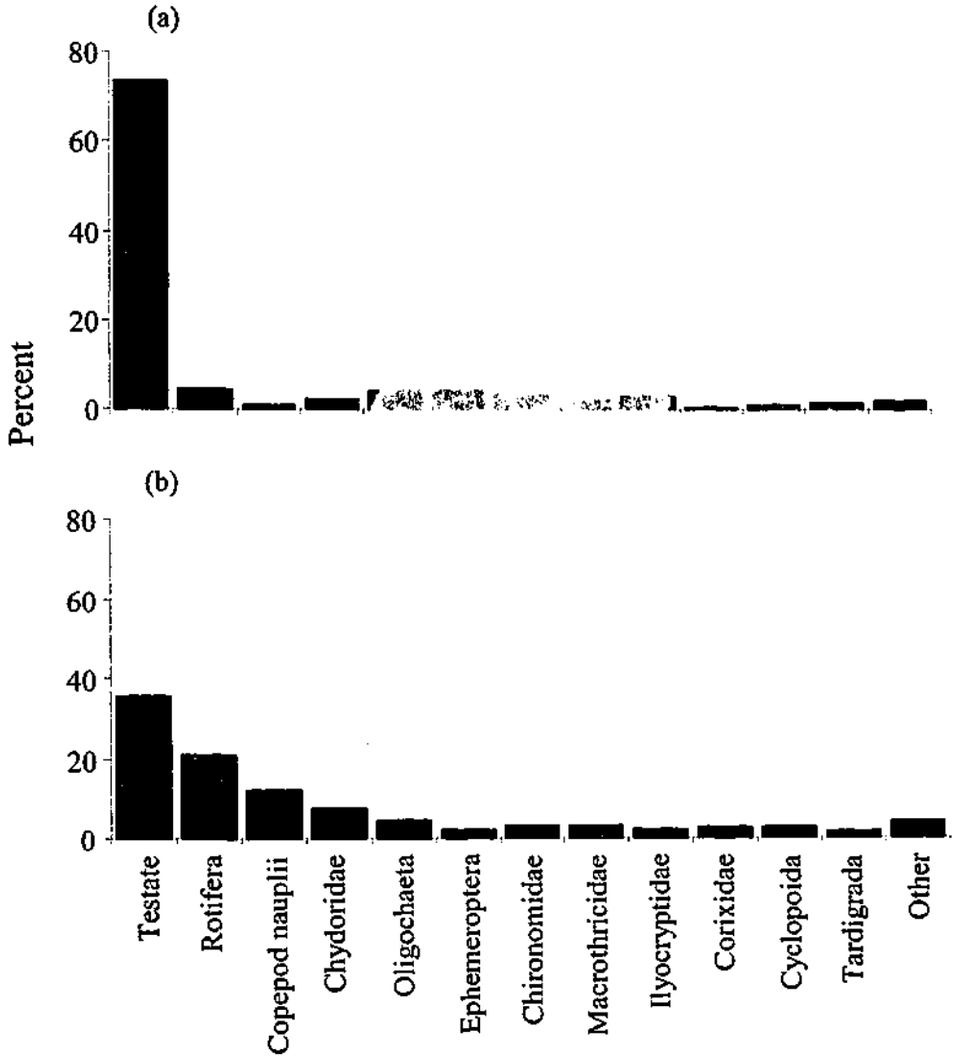


Figure 6.2: Percentage composition of (a) epibenthic and (b) pelagic fauna, showing main contributing taxa.

There were highly significant differences in the composition of the community between the two zones (MRPP: $P < 0.001$, $A = 0.427$, Figure 6.3a) and between sampling trips (MRPP: $P < 0.001$, $A = 0.058$, Figure 6.3b), but not between day/night or among habitat types (MRPP: day/night $P > 0.05$, $A = -0.005$; habitat $P > 0.05$, $A = 0.008$). The ordination analysis revealed a distinct separation between the community composition in the epibenthic and pelagic zones (Figure 6.3a). The epibenthic samples grouped tightly together, compared with the wider spread of the pelagic samples, indicating a greater variety in the composition of the pelagic than the epibenthic samples. The epibenthic zone was characterised by benthic-orientated taxa such as ilyocryptids, harpacticoids, oligochaetes, ephemeropterans and chironomid larvae, whereas the pelagic zone was characterised by rotifers and copepod nauplii (Figure 6.2, Indicator Species Analysis: $P < 0.001$). Community composition also differed significantly between the first sampling trip and the other three sampling trips (Figure 6.3b), mainly due to greater abundances of daphniids and simuliids in the November sampling trip than the other trips, and increases in the abundance of ilyocryptids, corixids, and trichopterans over time.

Community composition in the epibenthic zone varied significantly both with sampling trip and habitat type (MRPP: trip $P < 0.001$, $A = 0.195$; habitat $P < 0.001$, $A = 0.120$; Figure 6.4a & b), but there was no difference in the community composition between day and night (MRPP: $P > 0.05$, $A = -0.005$, Figure 6.4c). The composition of the epibenthic community was significantly different between each of the sampling trips (MRPP: all pairwise comparisons $P < 0.001$, Figure 6.4a). Whilst there was a gradient corresponding to increasing velocity among the habitat types in the ordination, there was no significant difference in the composition of the fauna between each of the six habitat types (MRPP: all pairwise comparisons $P > 0.05$, Figure 6.4b).

Community composition in the pelagic zone also varied significantly among sampling trips (MRPP: $P < 0.001$, $A = 0.248$, Figure 6.5a), but not among habitat types or between day and night samples (MRPP: habitat $P > 0.05$, $A = 0.049$; day/night $P > 0.05$, $A = 0.010$; Figure 6.5b & c). The composition of the pelagic zone fauna was significantly different between most of the sampling trips (MRPP: pair-wise comparisons $P < 0.05$), but not between the third and the fourth trip (MRPP: $P > 0.05$, $A = 0.056$, Figure 6.5a). Whilst there was no overall effect of habitat type, there was a similar increasing velocity gradient in the ordination, as was seen in the epibenthic fauna analysis (Figure 6.5b).

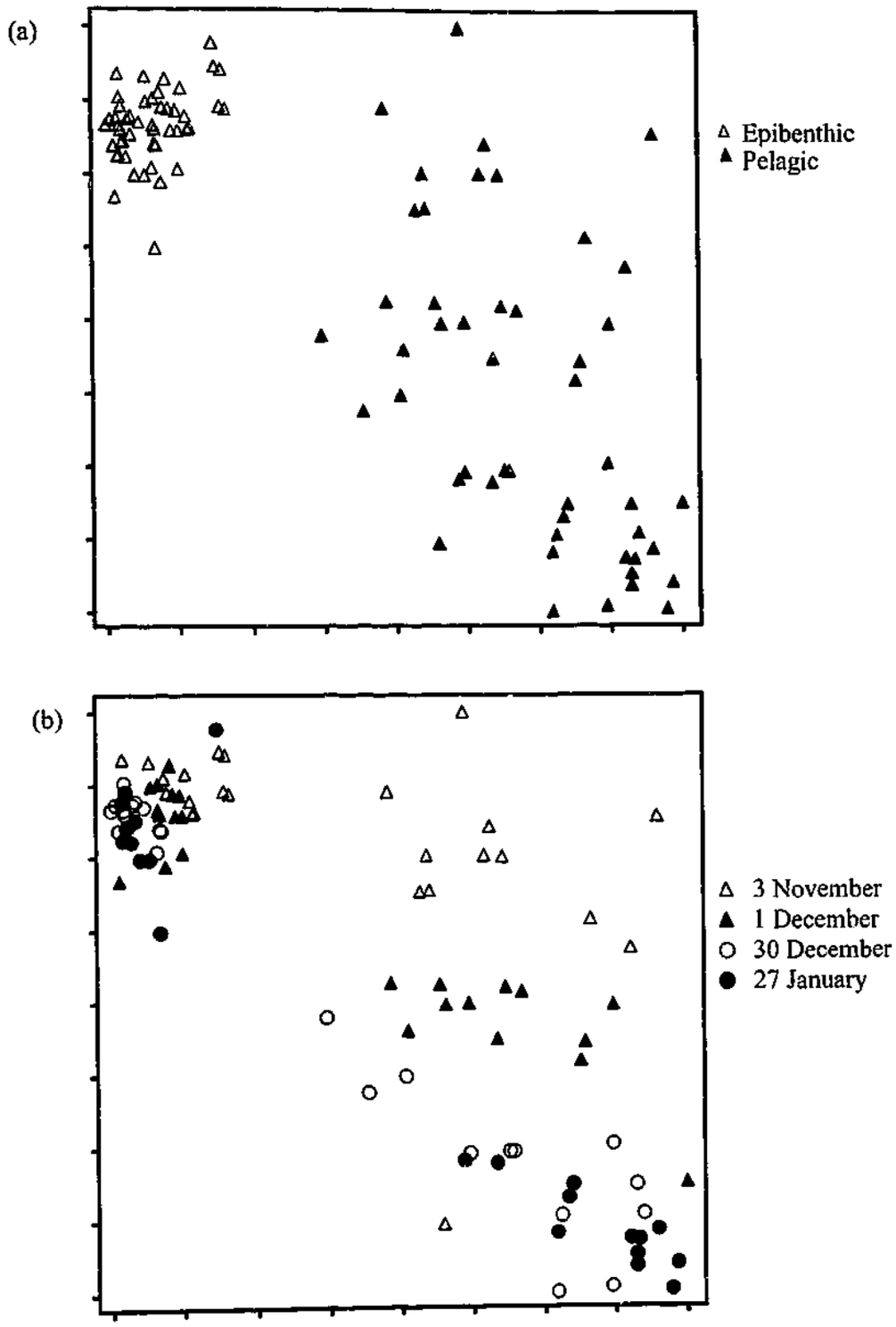


Figure 6.3: Two-dimensional solution for NMDS of the mean abundance of all taxa, from all sampling trips, in the epibenthic and pelagic samples. The ordination is presented to show groupings of (a) zone and (b) sampling trip. (30 random starts, maximum of 200 iterations, minimum stress = 0.077).

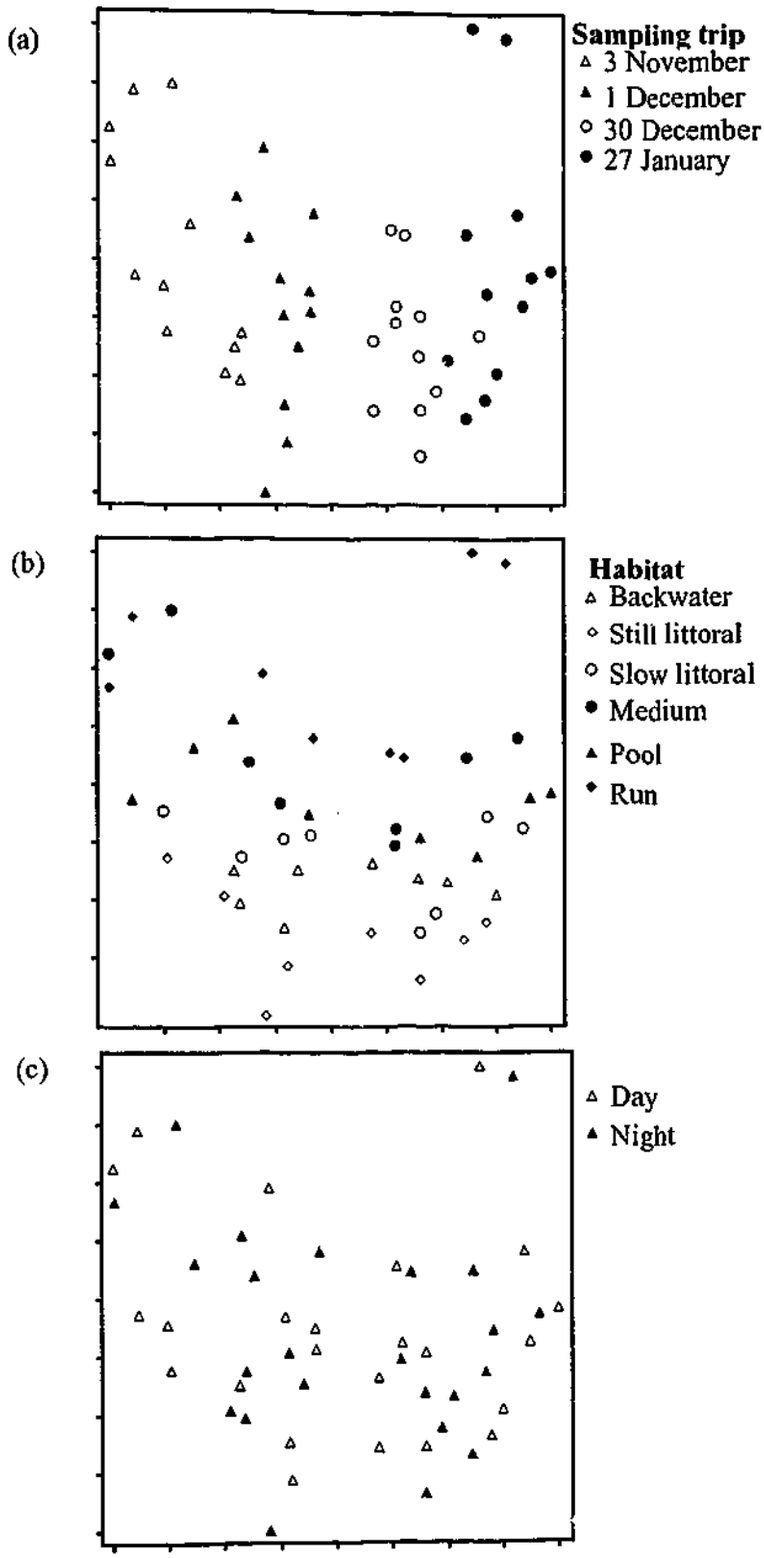


Figure 6.4: Two-dimensional solution for NMDS of the mean abundance of all taxa in the epibenthic zone. The ordination is presented to show groupings of (a) sampling trip, (b) habitat type and (c) day/night. (30 random starts, maximum of 200 iterations, minimum stress = 0.154).

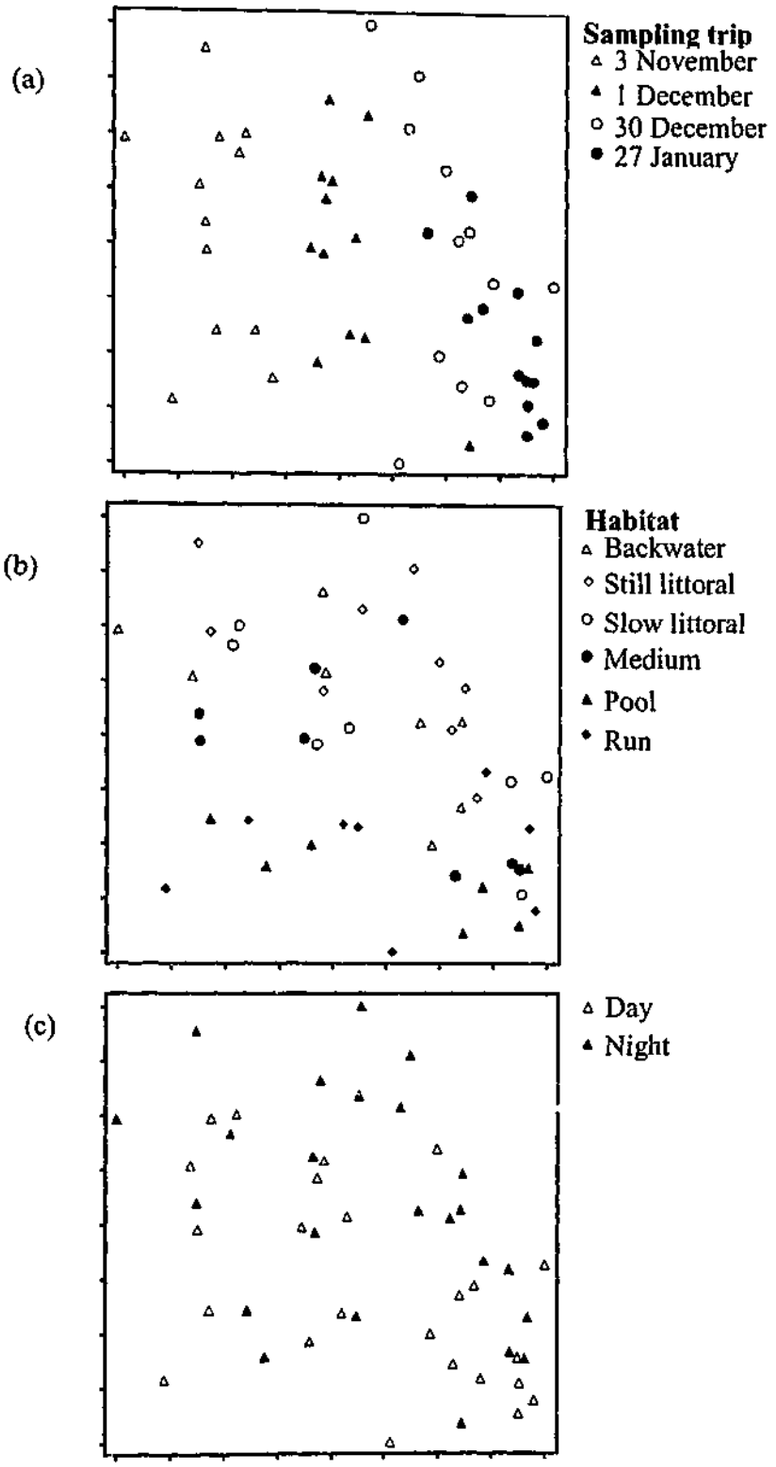


Figure 6.5: Two-dimensional solution for NMDS of the mean abundance of all taxa in the pelagic zone. The ordination is presented to show groupings of (a) sampling trip, (b) habitat type and (c) day/night. (30 random starts, maximum of 200 iterations, minimum stress = 0.105).

Variation in abundance

The effect of 'zone' explained by far the greatest amount of variance in the densities of total fauna and total fauna excluding testates (Table 6.2, $P < 0.001$). The density of the epibenthic fauna was, on average two orders of magnitude greater than the pelagic zone fauna, for both total fauna and total fauna excluding testates (Table 6.1, Figure 6.6 & 6.7). There were also significant effects of 'trip', 'habitat', 'day/night' and the interactions between 'zone' and 'habitat', and 'zone' and 'trip' (Table 6.2), but they all contributed very little to the overall variance. The average density of total fauna in the epibenthic zone increased through consecutive sampling trips, while the density of pelagic fauna decreased (Figure 6.6a). This pattern was also similar for total fauna excluding testates, where the average density of epibenthic fauna remained constant between successive sampling trips, while the density of pelagic fauna again decreased (Figure 6.6b).

Table 6.2: Mean squares and significance levels for results of 4-way analysis of variance of $\log_{10}$ transformed densities of total fauna and total fauna excluding testates, with 'zone', 'trip', 'habitat' and 'day/night' (DN) as factors. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	df	Total fauna		Total fauna excluding testates	
Zone	1	310.31	***	276.13	***
Trip	3	0.20	*	4.52	***
Habitat	5	0.46	***	0.46	***
DN	1	0.57	**	0.97	**
Zone * Trip	3	3.93	***	4.01	***
Zone * Habitat	5	0.60	***	0.87	***
Zone * DN	1	0.00		0.10	
Trip * Habitat	15	0.14	*	0.10	
Trip * DN	3	0.12		0.12	
Habitat * DN	5	0.07		0.09	
Zone * Trip * Habitat	15	0.11	*	0.09	
Zone * Trip * DN	3	0.09		0.20	
Zone * Habitat * DN	5	0.03		0.05	
Trip * Habitat * DN	15	0.04		0.06	
Zone * Trip * Habitat * DN	15	0.01		0.04	
Error	192	0.06		0.08	

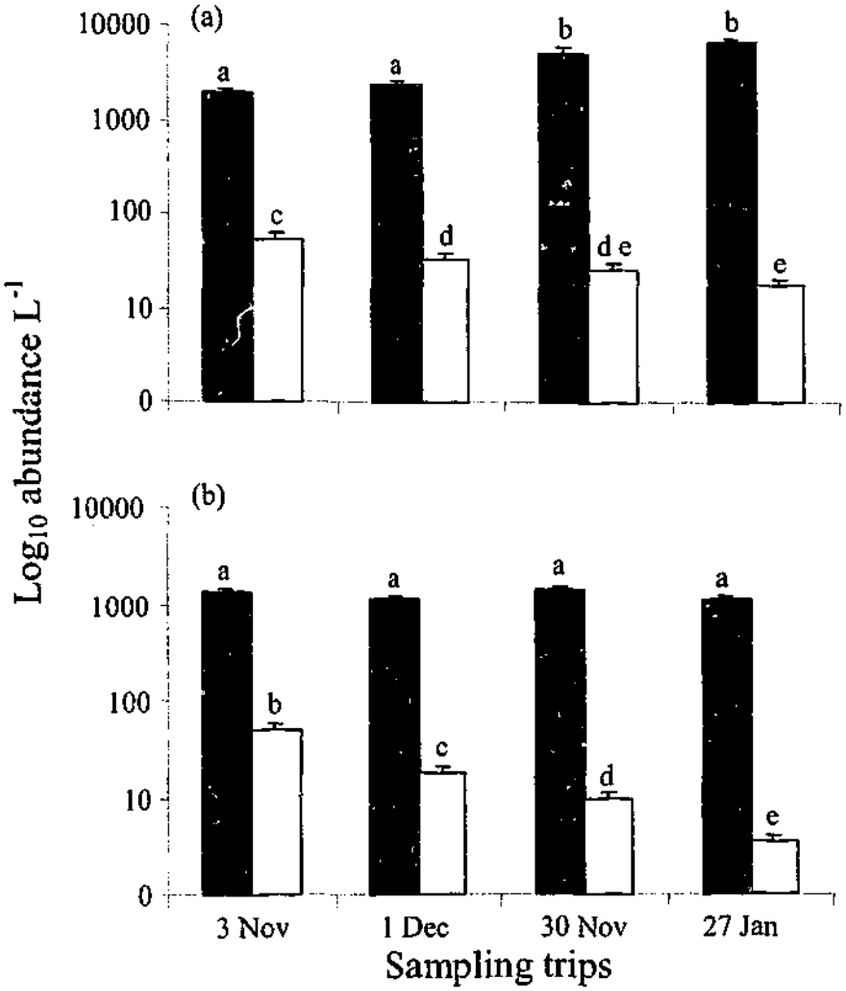


Figure 6.6: Mean (+ 1 SE) $\log_{10}$ abundance L^{-1} of (a) total fauna and (b) total fauna excluding testates in epibenthic (solid bars) and pelagic (clear bars) zones across the four sampling trips. Within each figure, the same letter indicates no significant difference between means.

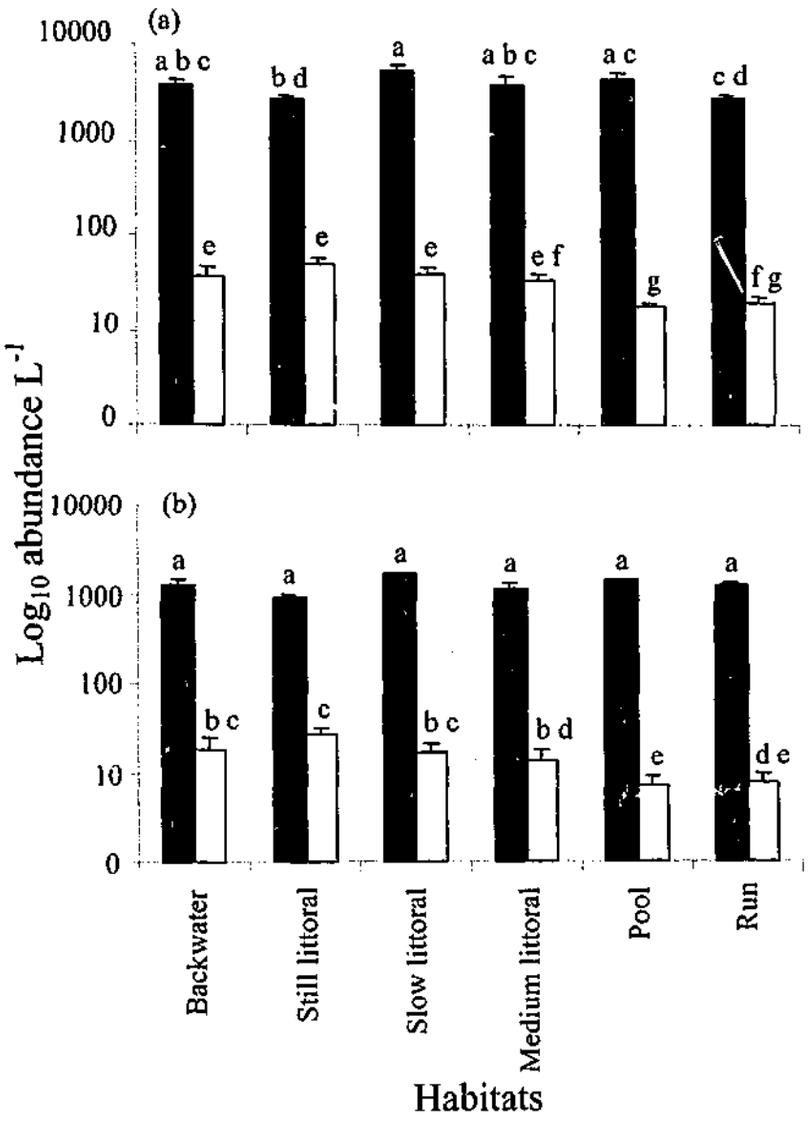


Figure 6.7: Mean (+ 1 SE) $\log_{10}$ abundance L^{-1} of (a) total fauna and (b) total fauna excluding testates in epibenthic (solid bars) and pelagic (clear bars) zones across the six habitat types. Within each figure, the same letter indicates no significant difference between means.

In general, the average density of epibenthic fauna remained constant between the six habitat types for both the total fauna and total fauna minus testates (Figure 6.7). However, there was a significant difference in density of pelagic meiofauna between the three littoral habitats and backwaters and the two mid channel habitats (pools and runs), for both total fauna and total fauna minus testates ($P < 0.001$, Figure 6.7).

The main prey items for larval and juvenile fish (see Chapter 5), namely rotifers, chydorids, macrothricids, cyclopoids, copepod nauplii and chironomid larvae, all had significantly greater densities in the epibenthic zone than in the pelagic zone (Table 6.3, Figure 6.8 & 6.9). All main prey items differed significantly in their densities between consecutive sampling trips, but differed in the pattern of density changes between successive sampling trips ($P < 0.001$, Figure 6.8). For example, while rotifers, chydorids and chironomids all decreased in density in both epibenthic and pelagic zones through time, there was no consistent pattern for macrothricids, cyclopoids or copepod nauplii.

All main prey items also differed significantly in their abundance among habitat types between the two zones ($P < 0.01$, Figure 6.9), although there was no consistent pattern across all taxa. There was more variation in the densities of epibenthic fauna among the habitat types, than for the pelagic fauna. None of the main prey items had significantly greater densities in backwater and still littoral habitats, than in the other habitat types (Figure 6.9). In general, the effect of 'day/night' explained very little of the variance of the main prey items (Table 6.3). However, the abundance of macrothricids, copepod nauplii and chironomids were all significantly greater at night than during the day ($P < 0.05$).

Table 6.3: Mean squares and significance levels for results of 4-way analysis of variance of log_{10} transformed densities of total Rotifera, Chydoridae, Macrothricidae, Cyclopoida, Copepod nauplii, and Chironomidae, with 'zone', 'trip', 'day/night' (DN) and 'habitat' as factors. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	df	Rotifera		Chydoridae		Macrothricidae		Cyclopoida		Copepod nauplii		Chironomidae	
Zone	1	129.86	***	96.37	***	85.45	***	51.40	***	48.89	***	233.25	***
Trip	3	10.32	***	15.64	***	7.36	***	5.02	***	2.98	***	0.67	***
DN	1	0.00		0.61		1.42	**	0.03		0.99	*	0.47	*
Habitat	5	1.23	***	4.47	***	5.58	***	2.34	***	2.07	***	0.30	*
Zone * Trip	3	1.79	***	2.55	***	3.15	***	4.05	***	4.34	***	0.27	
Zone * DN	1	0.66	*	0.12		0.18		0.70		0.53		0.28	
Zone * Habitat	5	1.32	***	0.84	***	3.17	***	1.12	***	1.08	**	0.53	***
Trip * DN	3	0.13		0.05		0.44		0.37		0.16		0.02	
Trip * Habitat	15	0.19		0.27		0.34	*	0.80	***	0.80	***	0.19	
Habitat * DN	5	0.25		0.08		0.14		0.08		0.20		0.02	
Zone * Trip * DN	3	0.39		0.17		0.15		0.08		0.22		0.09	
Zone * Trip * Habitat	15	0.21		0.29		0.41	*	0.36		0.47	*	0.17	
Zone * Habitat * DN	5	0.08		0.06		0.04		0.15		0.95		0.08	
Trip * Habitat * DN	15	0.11		0.06		0.11		0.13		0.34		0.03	
Zone * Trip * Habitat * DN	15	0.12		0.08		0.10		0.09		0.28		0.05	
Error	192	0.15		0.18		0.20		0.24		0.24		0.11	

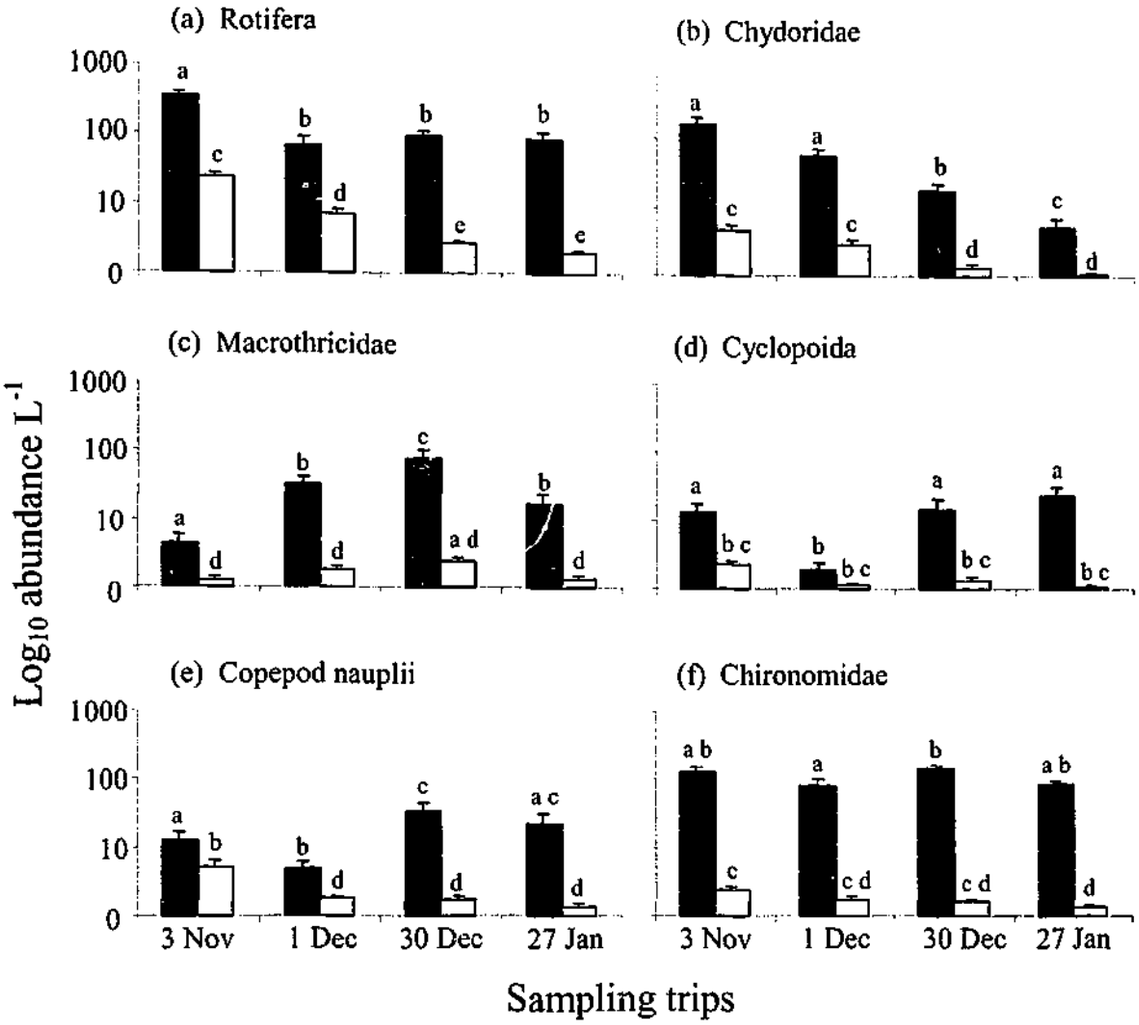


Figure 6.8: Mean (+ 1 SE) $\log_{10}$ abundance L^{-1} of (a) Rotifera, (b) Chydoridae, (c) Macrothricidae, (d) Cyclopoida, (e) Copepod nauplii and (f) Chironomidae for epibenthic (solid bars) and pelagic (clear bars) zones for all sampling trips. Within each figure the same letter indicates no significant difference between means.

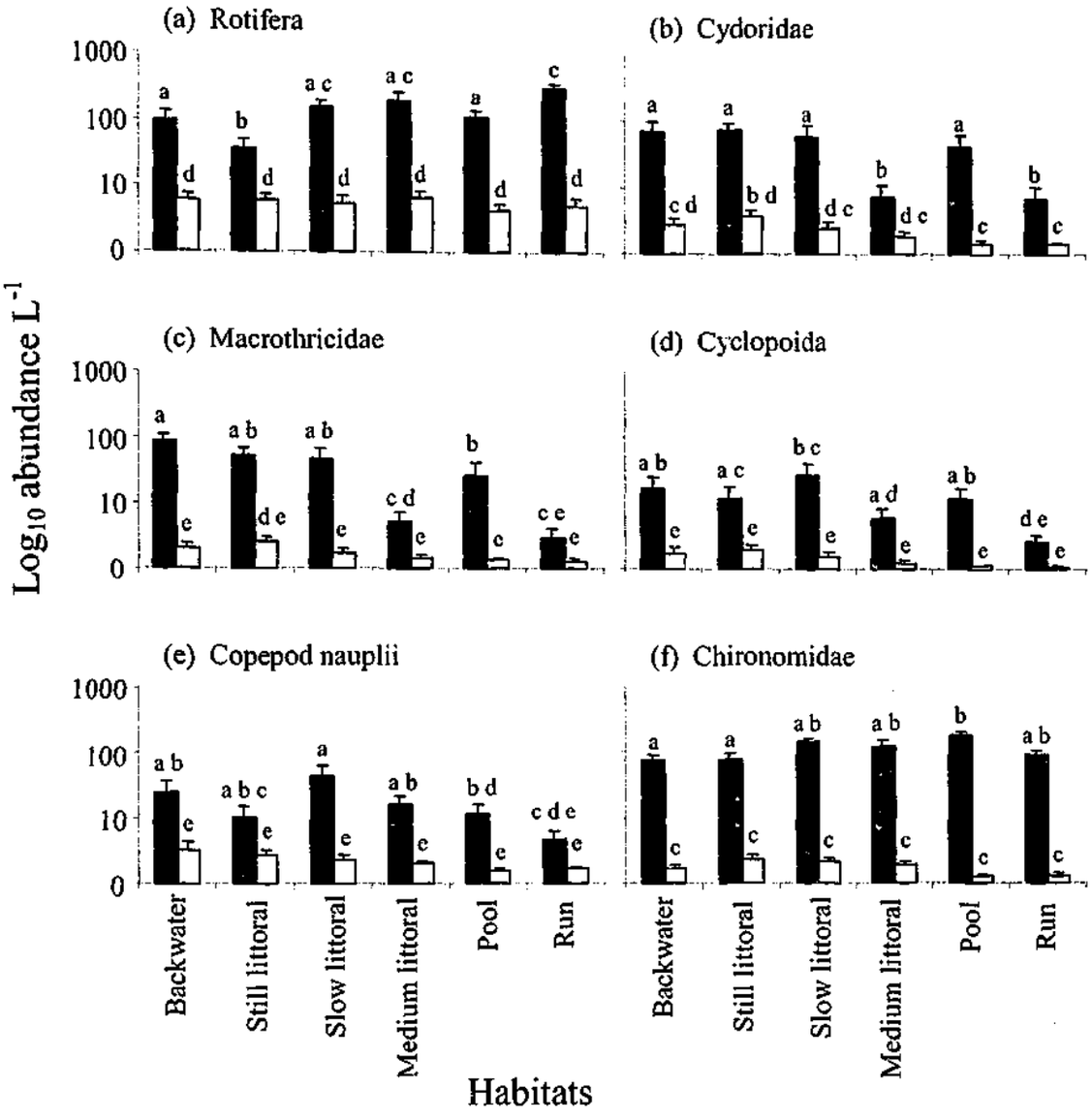


Figure 6.9: Mean (+ 1 SE) $\log_{10}$ abundance L^{-1} of (a) Rotifera, (b) Chydoridae, (c) Macrothricidae, (d) Cyclopoida, (e) Copepod nauplii and (f) Chironomidae for epibenthic (solid bars) and pelagic (clear bars) zones across the six habitat types. Within each figure the same letter indicates no significant difference between means.

6.4 Discussion

Meiofauna in the main channel environment

In marine systems, Cushing (1990) proposed that future recruitment strength is governed by the timing of the occurrence of larvae and the peak abundance of their prey. In riverine systems, similar hypotheses have suggested that successful fish recruitment will occur during periods of floodplain inundation, when large densities of potential prey items may become available (Lake 1967a, Welcomme 1985, Junk *et al.* 1989, Harris and Gehrke 1994, Schiller and Harris 2001). The importance of floodplain inundation for fish recruitment especially in Australia (eg. FRM), has stemmed from the assumption that the main channel does not provide high densities sufficient to sustain larval fish, and that the only environment where such densities do occur is on the inundated flood plain (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Schiller and Harris 2001).

The prey densities required for the survival of larval fish in Australian lowland rivers are not currently known. However, the required prey densities for larval survival in marine systems, have been proposed to vary between 100 and 1000 individual prey items L^{-1} for different species (Gerking 1994, Bone *et al.* 1995). As previously mentioned, an estimate of 500 individuals L^{-1} is commonly used as guide to maximise the chance of larval survival in the aquaculture rearing of Australian native freshwater fish (Ingram, B., Marine and Freshwater Resources Institute, Victoria, pers. comm.). In the present study, densities greater than an average of 1000 individuals L^{-1} occurred in the epibenthic zone. It is clear from the results of this study that sufficient densities do exist for successful larval survival within the main channel environment, and that this large potential food source can be found predominantly in the epibenthic zone.

A number of other studies have demonstrated that benthic microcrustacea in streams and rivers can attain high densities (Robertson 1990, Shiozawa 1991, Robertson *et al.* 1995, Robertson *et al.* 1997). Robertson (1990) found densities of chydorids peaked in summer in the River Thames, at around 45,000 individuals m^{-2}. The densities of benthic microcrustaceans in nine Minnesota streams, ranged from 16,652 to 430,863 individuals m^{-2} (Shiozawa 1991). Dettmers *et al.* (2001) sampled both the pelagic zooplankton and benthic macroinvertebrates in the main channel of the Illinois and

Mississippi Rivers, and found both types of fauna to be in sufficiently high densities to sustain the growth and survival of larval and juvenile fish in the main channel.

Traditionally, the densities of zooplankton in the main channel of rivers have been sampled in the pelagic zone only, using standard sampling techniques such as Schindler traps, pump samples or other quantitative devices. For example, zooplankton studies in the Murray and Darling Rivers, have demonstrated low average densities of zooplankton (< 150 individuals L^{-1}) in the pelagic zone of the main river (Shiel *et al.* 1982, Shiel 1985). By restricting sampling to the pelagic zone only, the total density and diversity of fauna within the main channel will be significantly underestimated. In the present study, meiofaunal densities were on average 100 times denser in the epibenthic zone than the pelagic zone. In addition, significant meiofaunal populations undoubtedly occur associated with other surfaces such as woody debris and macrophytes. As these surfaces were not sampled in the present study, the estimates presented here are also probably underestimates of the total abundance.

The composition of the meiofaunal community in the epibenthic and pelagic zones were distinct. The epibenthic zone was characterised by typically benthic-orientated taxa such as ilyocryptids, harpacticoids, oligochaetes, ephemeropterans and chironomid larvae, whereas the pelagic zone was characterised by rotifers and copepod nauplii. Interestingly, despite testates being a major component of the fauna found in both zones (overall 73% and 36% epibenthic and pelagic respectively), they were a very minor component of the diet of larval and juvenile fishes in the Broken River (see Chapter 5). Velho *et al.* (1999) also found that testates were the dominant zooplankters in littoral zones of both lentic and lotic environments in the flood plain of the Upper Parana River, Brazil. Another significant component of both the pelagic and epibenthic zones was the small (< 200 µm) first instar larvae of a number of taxa of "macroinvertebrates", such as chironomids, ephemeropterans and corixiids. These taxa were major components of the diet of larvae of a number of species, such as Murray cod and carp and were an important component in the diets of juveniles and adults for all species (see Chapter 5).

Distribution of potential prey among habitats

Fish larvae use still or slow flowing littoral areas, backwaters or shallow embayments as nursery habitats in the main channel of rivers (Moore and Gregory 1988a, Schiemer and Spindler 1989, Haines and Tyus 1990, Tyus 1991, Sempeski and Gaudin 1995, Wintersberger 1996, Watkins *et al.* 1997, see Chapter 4). One of the main reasons why these habitats have been proposed to be ideal nursery habitats is that they are thought to provide high densities of prey relative to other main channel habitats (Humphries *et al.* 1999). The LFRH suggests that an abundant alternative food source may exist in the epibenthic zone of these nursery habitats (Humphries *et al.* 1999). In the present study, the densities of pelagic fauna were slightly greater in littoral and backwater habitats than in main channel habitats, such as pools and runs, however, there was no significant difference in the densities of epibenthic meiofauna among the six habitat types.

Previous studies have suggested that due to the increased water residence time, non-flowing habitats contain greater densities of zooplankton than the main channel habitats of rivers (Thorp *et al.* 1994, Basu and Pick 1996, Reckendorfer *et al.* 1999, Reynolds 2000). For example, Reckendorfer *et al.* (1999) demonstrated that densities of zooplankton sampled in the pelagic zone were greater in inshore habitats with low flushing rates than in main channel habitats, and suggested that these habitats play a critical role in the maintenance of zooplankton populations in the main channel environment. Non-flowing habitats have also been hypothesised to support the production of plankton recruitment to the main channel (Reynolds 2000). Although the present study did detect a small decrease in density of pelagic fauna between littoral and main channel habitats, there was no difference in the abundance of epibenthic fauna among habitats. However, the present study did not attempt to determine whether the rates of production or recruitment of meiofauna in larval nursery habitats was greater, rather it only examined the overall densities present. This approach may mask the overall importance of these zones within the main channel for the production of meiofauna, especially since the densities recorded in this study may have been reduced in the larval fish nursery habitats relative to the other habitats, through predation. This could potentially be assessed by experimental manipulations of fish larvae in enclosures within the different habitats.

Abundances of prey taxa may differ in their densities among habitats in the main channel (Thorp *et al.* 1994, Bass *et al.* 1997) and this may potentially have important consequences

for growth and survival of larval fish (Bass *et al.* 1997, Mann *et al.* 1997). For example, Thorp *et al.* (1994) concluded that whilst overall densities of zooplankton were higher in littoral zones than in the main channel, rotifers were twice as abundant in the main channel habitats, while littoral habitats were dominated by copepods and cladocerans. Similarly, Dettmers *et al.* (2001), found slightly higher overall mean densities of zooplankton in backwaters than the main channel, although rotifers were dominant in the main channel and copepods were dominant in backwaters. The main prey items for larval and juvenile fish in the present study were rotifers, chydorids, macrothricids, cyclopoids, copepod nauplii and chironomid larvae (see Chapter 5). All of these taxa had significantly greater densities in the epibenthic zone than in the pelagic zone, but there were no significant differences in their densities between the larval nursery habitats than those in the other habitat types. This suggests that other mechanisms may influence the choice of nursery habitats rather than the density of potential prey (see Chapter 4). However, non-flowing habitats such as backwaters and still littoral areas, may provide an environment where the capture of prey by larvae is more energetically profitable than in faster flowing habitats (Flore and Keckeis 1998).

Conclusion

Although further work is required to understand the mechanisms underlying the habitat choice of larvae within the main channel, this study has clearly demonstrated that there is an abundant prey source in the main channel environment, without inputs from the inundated floodplain environment. It has also demonstrated the importance of the fauna within the epibenthic zone as a potential prey source for larval fish and demonstrates that the significance of epibenthic meiofauna has been severely underestimated in many previous studies.

Chapter 7: Use of the Flood Plain for Fish Recruitment During Flood and Non-flood Conditions

7.1 Introduction

The interaction of a river and its flood plain is critical for the maintenance of a river's ecological, geomorphological and hydrological integrity (Junk *et al.* 1989, Poff *et al.* 1997). The 'flood pulse concept' (FPC), developed by Junk *et al.* (1989), postulated that the bulk of a river's productivity is derived from within the flood plain and not from downstream transport as proposed by the 'river continuum concept' (Vannote *et al.* 1980). The FPC also suggests that the predictable inundation of a river's flood plain is the major driving force for the maintenance of biotic diversity and the production of animal and plant biomass (Junk *et al.* 1989).

The FPC includes an emphasis of the role of the floodplain environment in the ecology of riverine fish, suggesting that the flood plain provides a suitable spawning environment, an abundance of food for all life stages and is critical for the overall production of riverine fish (Junk *et al.* 1989, Bayley 1991). Flooding is the major cue for breeding of most fish in tropical rivers throughout the world, where marked seasonal differences in temperature do not occur (Welcomme 1985). In temperate systems, however, the FPC stresses the importance of the coincidence of high temperatures and high flows for successful fish recruitment (Junk *et al.* 1989). Thus, good recruitment should occur in years when the rise in water level and temperature are coupled. Conversely, poor recruitment should occur if the flood either does not occur or retreats too quickly during spring or summer. The importance of the timing and duration of floods has been demonstrated in a number of temperate floodplain rivers (Finger and Stewart 1987, Killgore and Baker 1996, Galat *et al.* 1998, Sparks *et al.* 1998). From studies in the Mississippi River system, both Galat *et al.* (1998) and Sparks *et al.* (1998), stressed the benefit of long periods of floodplain inundation that occur when water temperatures are appropriate for spawning of native fish species. The timing of floodplain inundation can also have major affects on the composition of the fish community, with the relative dominance of spring or summer spawners varying between wet and dry years (Finger and Stewart 1987).

The perceived importance of floodplain inundation for fish recruitment in the Murray-Darling Basin has been extrapolated from overseas models (Welcomme 1985, Junk *et al.* 1989) and early aquaculture studies on the breeding biology of native fish (Lake 1967 a & b, Llewellyn 1971, 1973, 1974). In the commonly proposed model, termed the 'flood recruitment model' (FRM) by Harris and Gehrke (1994), flooding enhances recruitment by either acting as a cue for spawning, which has been suggested for species such as golden perch (Lake 1967a), or by indirectly enhancing survival of larval and juvenile fish by providing abundant habitat and food (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992, Lloyd *et al.* 1994, Schiller and Harris 2001). The second pathway suggests that species such as Murray cod, which do not require floods to cue spawning, may have enhanced recruitment during flood years, primarily due to an increase in available food.

Despite the perception that flooding is important for the maintenance of the Murray-Darling Basin's fish fauna, a growing body of evidence questions the validity of some of the assumptions behind the FRM (Humphries *et al.* 1999). No published study as recorded larvae of any species of Murray-Darling native fish on the natural flood plain during flood periods. Despite this, Gehrke (1990a, 1991) conducted a series of experiments in artificial aquaculture ponds to examine the suitability of the flood plain for fish larvae. He found that golden perch larvae actively avoided artificial floodplain areas, suggesting that water quality had a greater influence on their distribution throughout the ponds than food availability. Further experiments also indicated that although golden perch larvae were attracted to the leachate of river red gum, a common riparian tree (Gehrke 1990b), the leachate could easily be in concentrations lethal to larval and juvenile golden perch in the natural environment (Gehrke *et al.* 1993).

A number of authors have proposed that, unlike the flood plain, the main channel of the Basin's floodplain rivers does not provide suitable densities of prey to sustain fish larvae through the critical first feeding period, and thus, the only environment suitable for larval survival is the inundated flood plain (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992). This assumption was recently questioned by Humphries *et al.* (1999) and has also clearly been challenged in previous chapters (see Chapters 5 and 6). Indeed, in previous chapters I have demonstrated that there are abundant potential prey items within the main channel environment, especially

within the epibenthic zone. In addition, Humphries *et al.* (in press) and I (see Chapter 4) have demonstrated that some native fish species are able to recruit within the main channel environment even during low flow periods.

Nevertheless, it is important to consider that a diversity of spawning and recruitment strategies may occur, and that some species could spawn in the main channel during non-flood years, but may also take advantage of the flood plain when it is inundated. This study aims to determine which species of fish utilise the flood plain as larvae, and which species recruit in floodplain environments during flood and non-flood years, in an unregulated river in the southern region of the Murray-Darling Basin. Specifically this study aimed to examine the timing of spawning relative to floods and the abundance and composition of the larval fish community during floodplain connection and isolation.

7.2 Materials and methods

Study site

The study was conducted in the lowland reaches of the Ovens River in north-east Victoria, Australia (Figure 2.1). The Ovens River is one of the last remaining unregulated rivers in the southern region of the Basin. The river also retains a large proportion of its natural river red gum forests, which cover most of the regularly inundated flood plain downstream of the regional city of Wangaratta. A detailed description of the river and the study site is given in section 2.3. A pilot study conducted in 1998 at three sites on the River, concluded that Peechalba in the Lavis Bend State Forest (146° 14' 30''S, 36° 9' 60''E), was the most accessible and feasible site for the full study (see Appendix D).

Sampling design

Sampling was conducted over one day, every two weeks from September to December 1999 (six sampling trips), and September to December 2000 (seven sampling trips). During the 1999 sampling season, the river broke its banks briefly (3 days duration) in early September, but remained within its banks through the rest of the period (Figure 2.9b). In 2000, three more protracted (19, 16 and 6 days duration respectively) and higher floods occurred during the study period (Figure 2.9c), with the largest flood occurring in late October.

The pilot study conducted in 1998, trialed the use of four commonly used larval sampling gears, light traps, sweep nets, drift nets and hand trawls (Appendix D). Based on the results of the pilot study I chose to use the newly developed sweep net electrofishing (SNE), hand trawl and drift net methods for the full study. These methods were the same as those used in the main channel sampling (see Chapters 3 & 4 for construction and general use of the methods).

Sampling was stratified by three habitat types on the flood plain: billabongs, anabranch and the floodplain proper. Billabong and floodplain proper sampling locations were randomly selected depending on availability of the habitat type within a 4 km^2 region of the State Forest. Billabongs were defined as permanent (> 4 month duration) lentic water bodies, generally containing a variety of aquatic macrophytes, with an obvious vegetative boundary and shape. Anabranches were easily distinguished from the other habitats, as they were deeper, steeper sloped and had slower flow (Figure 7.1a). Anabranch samples were taken at random locations, at least 500 m apart, along one anabranch line running through the State Forest. Floodplain proper habitats were defined as temporary (< 1 month), generally lentic water bodies, which often contained flooded terrestrial vegetation and had no obvious boundaries (Figure 7.1b). Due to the temporary nature of these habitats, their sampling was restricted to flooded or recently flooded areas. The edges of the anabranch and potential billabong sites were identified and marked using tape and reflectors attached to trees during low flow times for easier identification during high flow conditions.

The SNE method was used to sample billabongs, anabranches and the floodplain proper in shallow (≤ 1.0 m depth) habitats. A hand trawl net was used in billabongs and anabranches only, and sampled the surface of the deeper water habitats. Each of usually ten replicate samples, were taken in different billabongs or locations on the flood plain on each trip. However, when either flooding hindered full access on the flood plain or when floodplain habitats dried up, the number of samples was necessarily reduced (Table 7.1). Due to practical considerations, sampling with the SNE and hand trawl methods was restricted to daylight hours only, and was conducted between 1000 and 1600 h. Drift net samples were collected during both the day and night to maximise the chance of collecting diurnal drifting species such as Murray cod (see Chapter 4). One drift net was placed in fast flowing water for 3 h, in both the anabranch and in the main channel of the river. Drift

sampling was conducted during the day between 1300 and 1600 h, and at night between 2000 and 2300 h in both habitats.

Table 7.1: Number of samples collected using each method in each habitat type, during 1999 and 2000. SNE = Sweep net electrofisher, Mch = Main channel, Ana = Anabranch, BB = Billabong, FL = Floodplain proper.

	Drift		SNE			Hand trawl	
Sampling date	Mch	Ana	BB	Ana	FL	BB	Ana
1999							
9 September	2	2	10	10	10	10	10
23 September	2	2	10	10	5	10	10
8 October	2	2	10	10	-	10	10
18 October	2	-	10	10	-	10	10
4 November	2	-	10	10	-	10	10
18 November	2	-	10	10	-	10	10
2000							
8 September	2	2	10	10	10	10	10
21 September	2	2	10	10	10	10	10
5 October	2	2	10	10	10	10	10
17 October	2	2	10	10	10	10	10
30 October	1	1	4	5	8	4	5
13 November	2	2	10	10	10	10	10
30 November	2	2	10	10	5	10	10

Dissolved oxygen concentration and water temperature were recorded at the location of each sample, using a Horiba™ U10 Water Quality Checker (Horiba Ltd, Japan). Turbidity, conductivity and pH were also measured using the Horiba™ at three randomly selected sampling points on each sampling trip. Only dissolved oxygen and temperature, which showed consistent patterns either among trips or habitats were analysed. Where no consistent patterns were observed, means and ranges are presented (Table 7.2).

Table 7.2: Minimum, maximum and mean (1 SE) values of water quality attributes measured during 1999 and 2000 sampling periods.

	1999			2000		
Parameter	Min	Max	Mean (SE)	Min	Max	Mean (SE)
Turbidity (NTU)	15.00	155.00	73.67 (9.22)	35.00	300.00	118.24 (20.72)
Conductivity ($\mu S\ cm^{-1}$)	40.00	90.00	60.00 (1.00)	40.00	180.00	60.00 (10.00)
pH	5.28	6.94	6.30 (0.13)	5.84	6.97	6.54 (0.06)
Temperature (° C)	12.50	24.00	17.67 (0.92)	10.20	25.50	16.49 (0.94)
Dissolved oxygen ($mg\ L^{-1}$)	1.60	9.90	6.76 (0.64)	0.70	9.22	6.34 (0.51)

(a)

(b)

Figure 7.1: (a) Anabranch habitats on Ovens River floodplain (Photo courtesy of T. Bowen, Murray-Darling Freshwater Research Centre) and (b) floodplain proper habitat on the Ovens River during flooding in October 2000.

Preservation and laboratory methods

All samples were preserved in 95% ethanol and returned to the laboratory. Fish were sorted and identified using a dissecting microscope. Identifications were made using published and unpublished descriptions and keys (Lake 1967b, McDowall 1996, Neira *et al.* 1998, P. Humphries, unpub. data., see Appendix A). The standard lengths of fish < 10 mm were measured using an eyepiece graticule, and fish > 10 mm were measured using vernier callipers, all to 0.1 mm. The developmental stage of each fish was determined using categories derived from both Ahlstrom *et al.* (1976) and Snyder (1976). These were: protolarvae (no curvature of the notochord in the caudal fin), postflexion (upward flexion of the notochord, caudal fin rays developing), metalarvae (caudal fin rays developed and pelvic fins beginning to form), and juvenile/adult (rays in all fins fully developed). Gambusia larvae, which are born live, were classified into two categories; postlarvae 1 (newly born larvae with no pelvic fin buds present) and postlarvae 2 (pelvic fin buds present). Murray cod larvae were also termed postlarvae, due to the advanced development of their fins, whilst still retaining their yolk sac.

Data analysis

Differences between water temperature and dissolved oxygen concentrations between the two sampling years were analysed using a 3-way analysis of variance (ANOVA); with 'year', 'trip' and 'habitat' as fixed factors. To create a balanced design, only the first six sampling trips in 2000 were used in the analysis, and floodplain habitats were excluded from the analysis. Within each sampling year, water temperature and dissolved oxygen differences among all habitats and sampling trips were established using 2-way ANOVA. *Post hoc* examination was conducted using Tukey's test. Dissolved oxygen concentrations were converted to percent saturation and arcsine transformed before analysis. The normality and homogeneity of variances of the data were checked by examining probability plots compared with normal distributions in SYSTAT™ (Wilkinson 1990), but water temperature data did not require transformation.

The initial description of the fish captured during sampling is presented as raw data. All other comparisons are adjusted for different sampling efforts (Table 7.1), to a standard ten samples from the three habitat types for both the SNE and hand trawl methods for each trip. Spearman rank correlation tests were conducted on the total abundance of all larvae and the average daily discharge on the sampling date, and one, two and three weeks prior

to the sampling date. The abundance of larvae captured by drift net sampling was standardised to the number of larvae per 1000 m^3 of filtered water. Although drift sampling was conducted both during the day and at night to maximise the likelihood of capturing known nocturnal drifting species such as Murray cod, day and night samples have been combined. Only five taxa, carp, Australian smelt, redfin perch, carp gudgeons and gambusia, were collected in sufficient numbers in both years to determine their response to different flow heights and their habitat preference within the floodplain environment.

Habitat associations of the five dominant species were described for five method/habitat combinations. These were: SNE anabranch (edge habitats of anabranches sampled with the SNE method), SNE billabong (edge habitats of billabongs sampled with the SNE method), SNE flood plain (floodplain proper habitats sampled with the SNE method), hand trawl anabranch (surface of deeper water in anabranches sampled with the hand trawl method) and hand trawl billabong (surface of deeper water in billabongs sampled with hand trawl method).

Due to the uneven sampling design between trips and years, and the patchiness of larval abundance with time, the data did not fully conform to the assumptions of normality required for analysis using parametric statistics. Therefore, the habitat preferences of fish larvae within the floodplain environment were analysed using an index of habitat association (I_{HA}) (similar to the procedure used in Chapter 4). This is based on a similar procedure described by Bult *et al.* (1998). The index was calculated using the formula:

$$I_{HA} = \log_{10}(\text{Obs} + 1) - \log_{10}(\text{Avg. R} + 1)$$

Where Obs = total number of fish collected within each habitat category of the observed data, and R = the randomised total number of fish within each habitat category. 'R' was generated using a randomisation procedure, where the observed number of fish per sample were randomly rearranged in the data matrix, and the total number of fish within each habitat type in the randomly generated data is then calculated (Crowley 1992, Potvin and Roff 1993, Sokal and Rohlf 1995). The randomisation procedure was performed using Visual Basic™ (Excel 97™) scripts. The I_{HA} varies around zero, but is not confined to any range. A positive I_{HA} value indicates a positive association with that habitat type, and a

negative I_{HA} value indicates a negative association. To calculate the significance level of the I_{HA}, the rank of each of the observed data values was established within the generated randomised distribution (Sokal and Rohlf 1995). A total of 1000 randomisation runs were used to determine both the I_{HA} and the statistical significance of the observed data. This distribution free randomisation approach to the analysis allowed all data to be considered in the model and did not require the strict assumptions of other statistical procedures. Only sampling trips where the larvae of particular species were present were used in the analysis for that species.

7.3 Results

Water temperature and dissolved oxygen

Water temperature was significantly higher during 1999 than in the 2000 sampling period ($P < 0.001$, Table 7.3, Figure 7.2a). Water temperature also increased significantly throughout the study period in both 1999 and 2000 ($P < 0.001$). There was no significant difference between habitat types overall, however there was a significant interaction effect of 'year' and 'habitat' ($P < 0.001$). In 1999, temperature was on average higher in anabranch habitats than in billabongs ($P < 0.001$). This pattern was reversed in 2000, where both billabongs and the floodplain proper were slightly warmer than anabranch habitats ($P < 0.001$). There was no significant difference between the water temperatures in the floodplain proper and billabongs during the 2000 sampling ($P > 0.05$).

Table 7.3: Mean squares and significance levels for results of 3-way analysis of variance on temperature and dissolved oxygen saturation data, with 'year', 'trip' and 'habitat' as factors. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, df = degrees of freedom.

Factor	df	Temperature		Dissolved oxygen	
Year	1	335.56	***	4.83	
Trip	5	351.64	***	37.44	***
Habitat	1	1.73		513.61	***
Year * Trip	5	17.61	***	2.38	
Year * Habitat	1	28.04	***	30.63	***
Trip * Habitat	5	1.49	*	14.14	***
Year * Trip * Habitat	5	4.59	*	9.63	***
Error	205	0.65		1.83	

Overall differences in percent saturation of dissolved oxygen were mostly explained by 'habitat' (Table 7.3). In both years, percent saturation of dissolved oxygen was significantly higher in anabranch habitats than billabong habitats ($P < 0.001$, Table 7.3, Figure 7.2b). While there was no significant difference in dissolved oxygen between sampling years, there were significantly greater levels of dissolved oxygen saturation in billabong habitats in 2000 than in the previous year (Figure 7.2b, $P < 0.001$). However, there was no significant difference in dissolved oxygen saturation in the anabranch habitats between the two years ($P > 0.05$). Dissolved oxygen varied significantly through time and across habitat types during both 1999 and 2000 ($P < 0.001$). In 1999, dissolved oxygen levels were generally significantly higher in anabranch habitats than billabongs ($P < 0.001$). While dissolved oxygen levels were consistently higher in the anabranch habitats than both the billabongs and the floodplain proper habitats throughout 2000 ($P < 0.001$), there was no significant difference between floodplain proper and billabong habitats ($P > 0.05$).

Fish community composition

A total of 1263 larvae and 504 juveniles/adults from six species were captured on the floodplain environment in 1999, and 1609 larvae and 331 juveniles/adults from 11 species during the sampling in 2000 (Table 7.4). In 1999, only four species were collected as both larvae and juveniles/adults, while in 2000, six species were captured as both larvae and juveniles/adults. An additional five species; mountain galaxiid, Murray jollytail, southern pygmy perch, Murray cod and oriental weatherloach; were caught as larvae in 2000 compared to 1999. However, little information about their spawning preferences could be inferred, since they were caught in very low numbers (≤ 2 individuals each, Table 7.4).

In 1999, 74.3%, 24.7% and 1.0% of larvae were captured in the hand trawl, SNE and drift net methods, respectively, while in 2000, the three methods captured 48.6%, 42.9% and 8.5%, respectively. The species composition of larvae, captured by both the SNE and hand trawl methods, differed between the two years and among sampling trips (Figure 7.3). Australian smelt were dominant in all sampling trips in 1999 (Figure 7.3a), with the exception of the final sampling trip on 18 November, which was dominated by carp gudgeons. Australian smelt larvae dominated in the first four sampling trips of the 2000

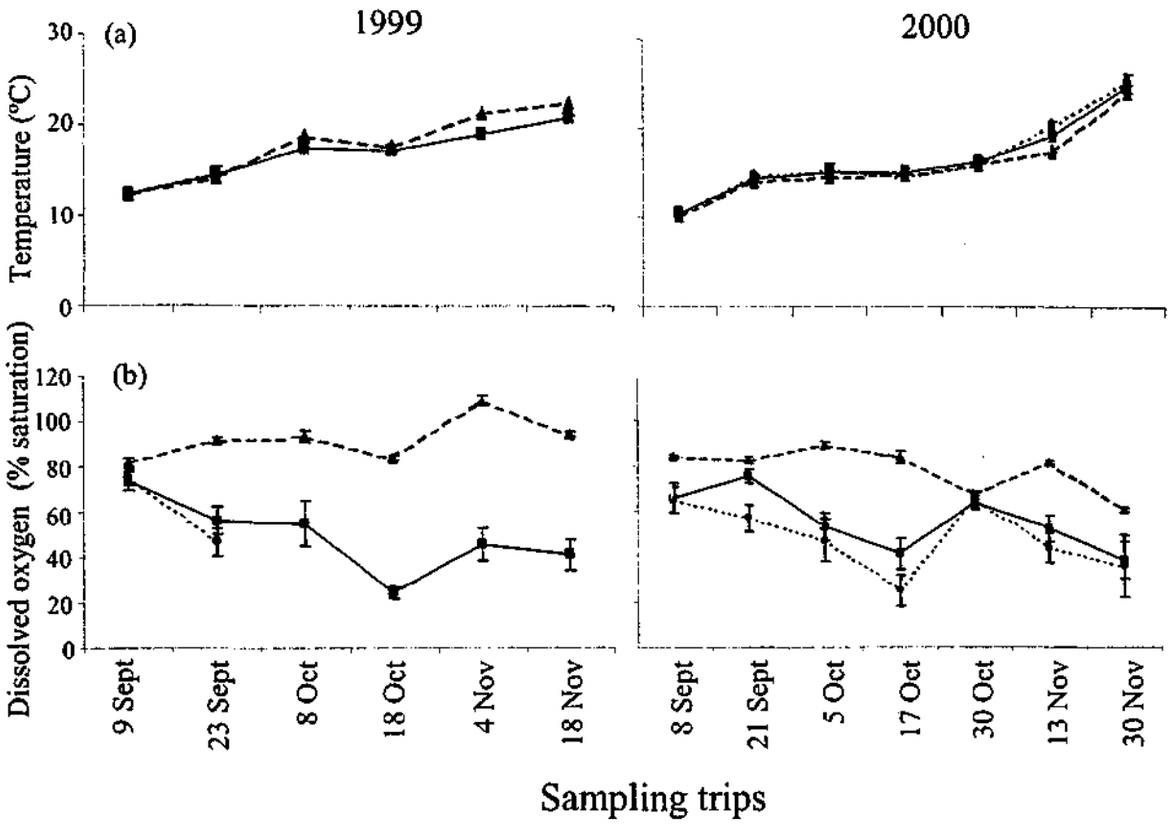


Figure 7.2: Mean (± 1SE) (a) temperature and (b) percent dissolved oxygen saturation for 1999 and 2000 sampling trips in —■— billabong, --▲--- anabranch and ···●··· floodplain habitats.

Table 7.4: Number of larvae and juvenile/adults of each species captured in 1999 and 2000, between the three methods (drift, SNE and hand trawl) and habitat types. All data (including drift) are presented as unadjusted raw data. Ana = Anabranch, Mch = main channel, BB = Billabong, FL = Floodplain, * = introduced species.

			1999								2000							
			Drift		SNE			Hand trawl		Total	Drift		SNE			Hand trawl		Total
Common name	Stage	Length range (mm)	Ana	Mch	Ana	BB	FL	Ana	BB		Ana	Mch	Ana	BB	FL	Ana	BB	
Carp *	Larvae	3.8 – 18.9		2	58	138		3	10	**211**	48	73	72	171	245	14	50	**673**
	Juveniles	14.1 – 46.6			1	15				**16**			2	19	12	1		**34**
Australian smelt	Larvae	4.1 – 20.2			42	18		148	578	**786**		3	59	46	20	80	346	**554**
	Juvenile/adults	18.4 – 51.0	2			2			34	**38**	1	1		1		19	3	**25**
Redfin perch *	Larvae	5.6 – 11.6	5	5	4		1		2	**17**	2	4	3	1	1		7	**18**
	Juveniles	21.6 – 31.7											1	1				**2**
Carp gudgeons	Larvae	1.7 – 11.2			3	3		30	167	**203**	2	2	6	12		4	277	**303**
	Juvenile/adults	11.5 – 39.9	6	3	219	5		2	2	**237**	9	3	153	14	6	2	2	**189**
Gambusia *	Postlarvae	6.2 – 12.9				45			1	**46**			9	20	21		3	**53**
	Juvenile/adults	8.0 – 41.7			18	171	1		20	**210**			17	18	15		1	**51**
Flathead gudgeon	Juvenile/adults	30.1 – 48.2			2	1				**3**	2	2	24	1				**29**
Mountain galaxiid	Larvae	12.4 – 13.0													1	1		**2**
	Juveniles	24.2															1	**1**
Murray jollytail	Larvae	10.4 – 11.6									1		1					**2**
Southern pygmy perch	Larvae	8.1													2			**2**
Murray cod	Postlarvae	10.1									1							**1**
Oriental weatherloach *	Larvae	25.5													1			**1**
	Total Larvae		5	7	107	204	1	181	758	**1263**	54	82	150	250	291	99	683	**1609**
	Total Juvenile/adult		8	3	240	194	1	2	56	**504**	12	6	197	54	33	22	7	**331**
	Total fish		13	10	347	398	2	183	814	**1767**	66	88	347	304	324	121	690	**1940**
	No. samples		6	12	60	60	15	60	60		13	13	65	64	63	65	64	
	No. fish per sample		2.17	0.83	5.78	6.63	0.13	3.05	13.57		5.08	6.77	5.34	4.75	5.14	1.86	10.78	

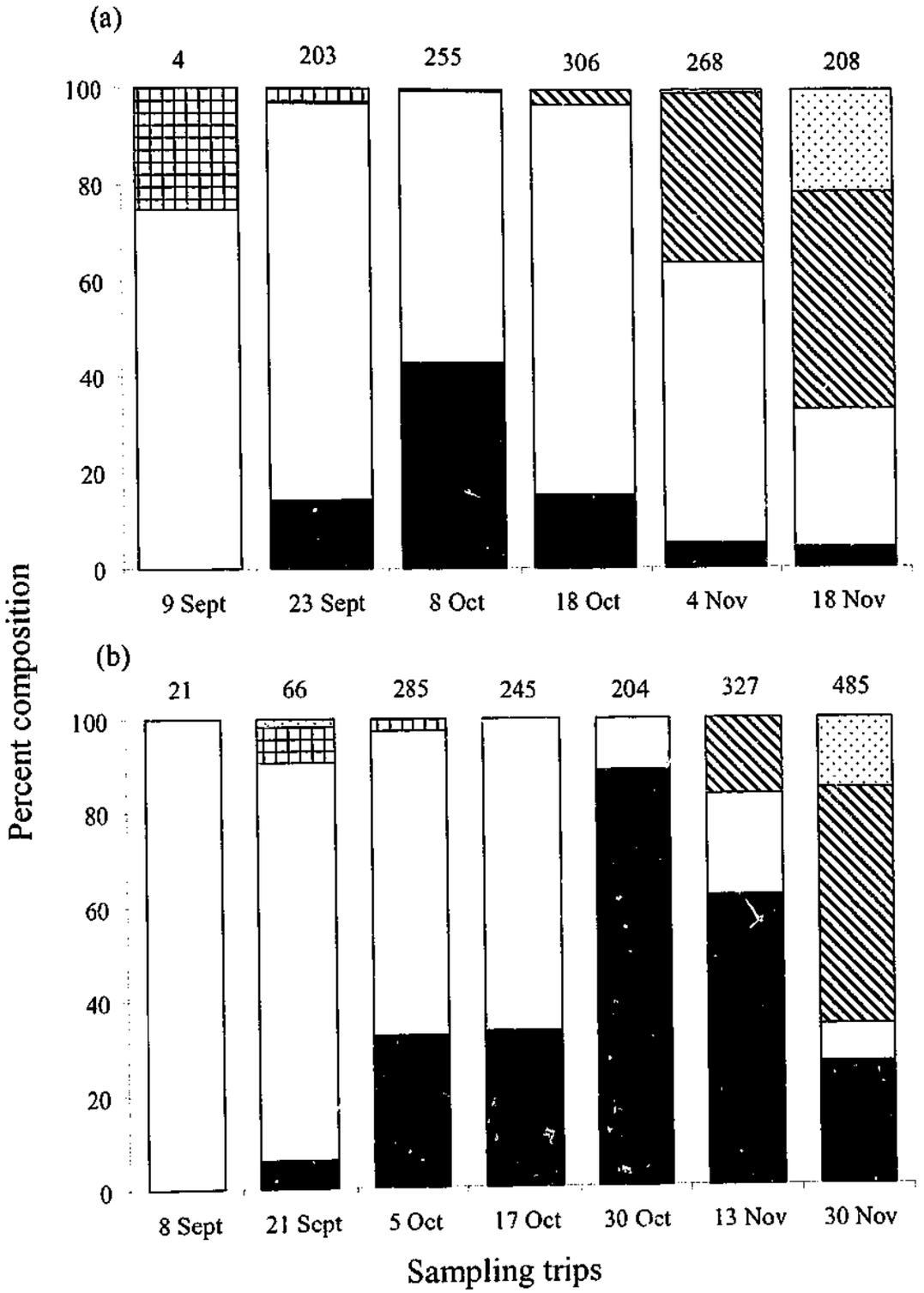


Figure 7.3: Larval fish composition for (a) 1999 and (b) 2000 sampling trips. Data does not include fish captured in drift net samples and is also adjusted for the different efforts between sampling trips. ■ carp, □ Australian smelt, ⊞ redfin perch, ⧅ carp gudgeons and ⊡ gambusia. Number above bar indicates total number of larval fish per sampling trip.

study period, however carp larvae dominated in the 30 October and 13 November sampling trips (Figure 7.3b). Carp gudgeons were again dominant in the final sample in late November.

A greater total abundance of larvae and number of species was captured in drift net sampling in 2000 than 1999 (Table 7.4). Drifting carp larvae were captured in both years, predominantly in the main channel drift samples, and were caught in much higher densities in 2000 (Figure 7.4). Redfin perch larvae were captured in both the main channel and anabranch samples in September in both sampling years. Australian smelt and carp gudgeons were captured in drift nets only in 2000, predominantly in the main channel samples (Figure 7.4).

Larval abundance and flow

The total abundance of larvae captured in the floodplain environment did not correlate with simultaneous or lagged (one, two or three weeks) discharge, in either 1999 or 2000 sampling seasons (Figure 7.5, Spearman's rank tests, $P > 0.05$). A similar number of larvae were captured from late September to late November during low flow conditions in 1999, whereas the peak abundance of larvae did not occur until early December in 2000, again during low flow conditions.

The timing and abundances of larvae of the five main species were generally similar between the two sampling years and were therefore not related to flood events (Figure 7.6). A peak in the abundance of carp protolarvae was found in early October in both years, but a stronger second peak was observed in late October 2000, associated with a period of floodplain inundation (Figure 7.6b). Australian smelt larvae were found throughout the entire sampling period in both years. Two major peaks in the abundance of Australian smelt protolarvae occurred in late September and late October 1999, but only one peak was observed in early October in 2000 (Figure 7.6c). This peak was followed by a dramatic decline in abundance during and after the late October flood. Redfin perch larvae were found in both years in early to mid-September in relatively low numbers (Figure 7.6d). Carp gudgeons first appeared as larvae in mid October in 1999, but were not collected until mid November in 2000 (Figure 7.6e). Gambusia were first collected in early November in 1999, but not until early December in 2000 (Figure 7.6f).

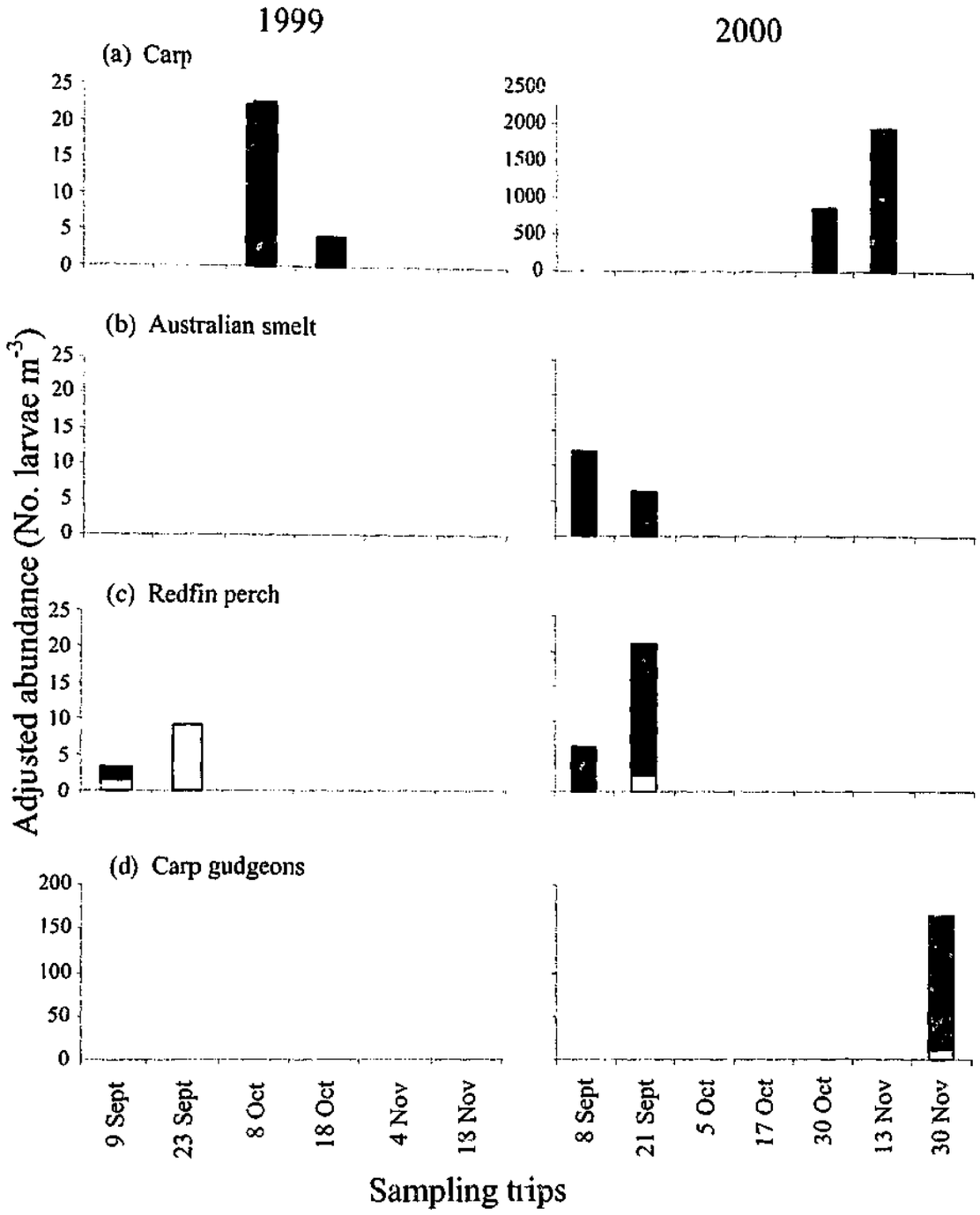


Figure 7.4: Adjusted larval abundance of (a) carp, (b) Australian smelt, (c) redfin perch and (d) carp gudgeons, in drift samples in the main channel (solid bars) and anabranch (clear bars) during 1999 and 2000 sampling trips. Note different y-axis scales. Only day drift net samples taken on 30 October 2000 sampling trip. Australian smelt and carp gudgeons captured in 2000 only.

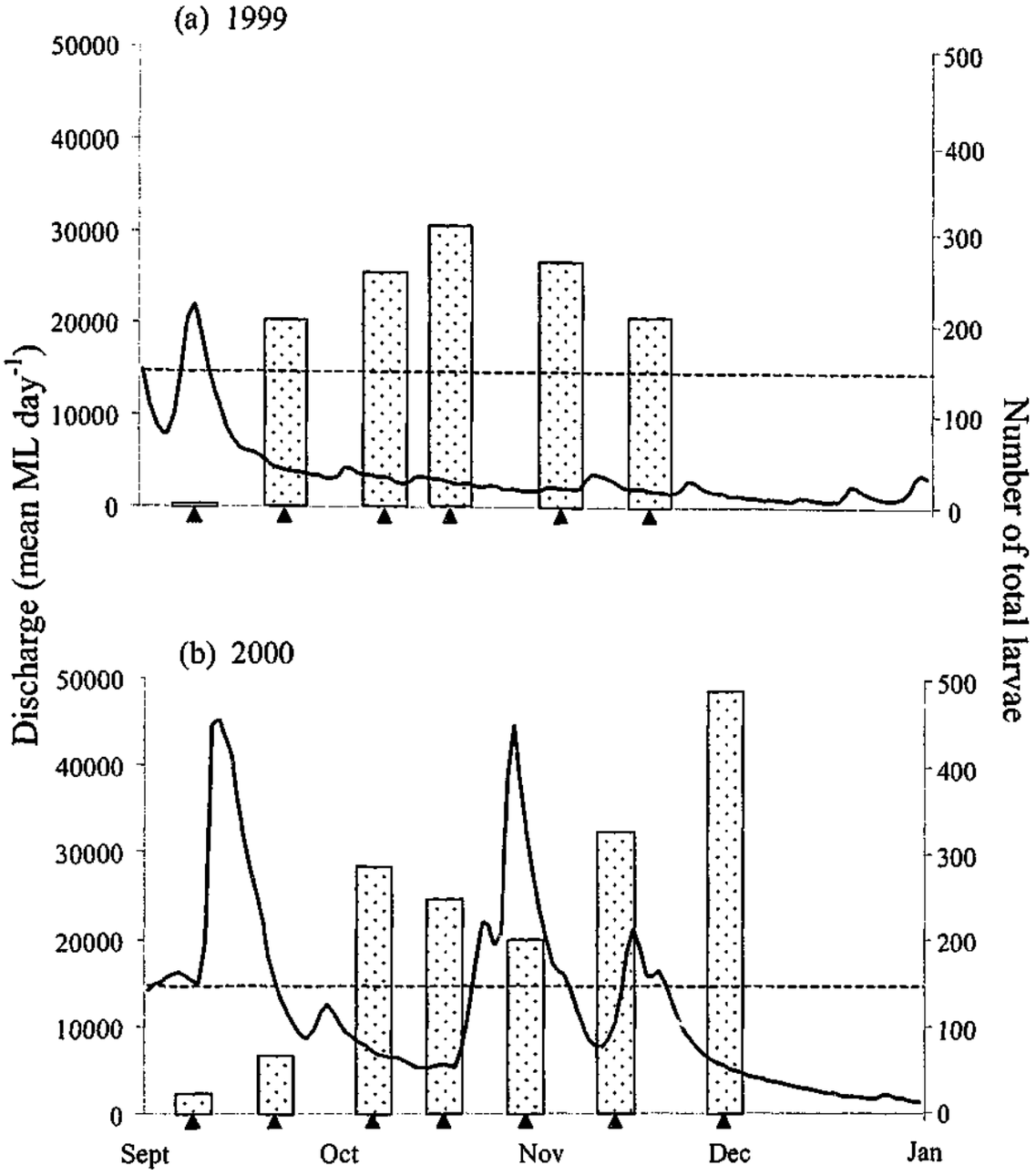


Figure 7.5: Discharge (solid line) and abundance of total larvae (speckled box) in (a) 1999 and (b) 2000, across sampling trips. ---- Floodplain inundation height, ▲ sampling trips.

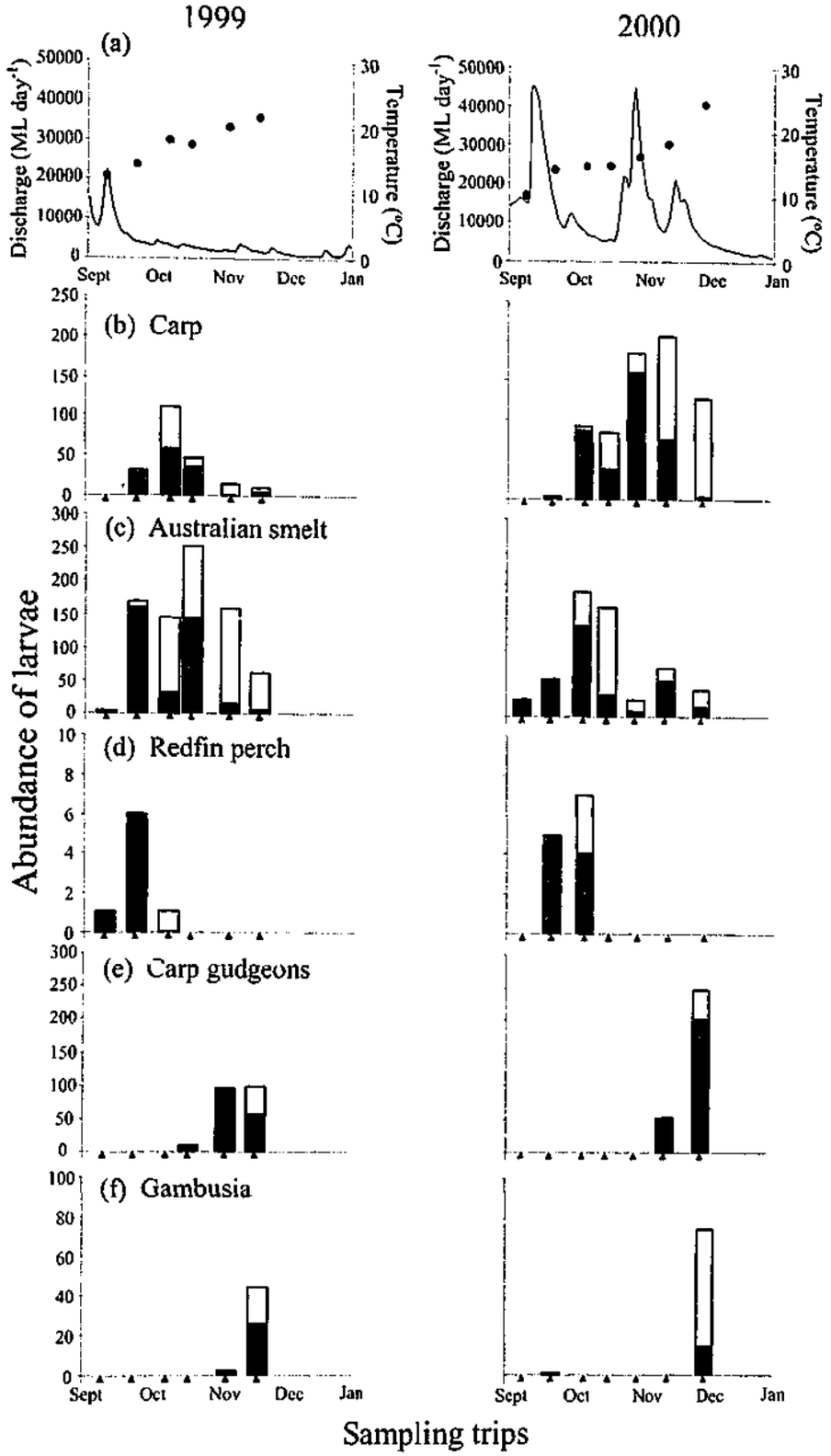


Figure 7.6: (a) Discharge (solid line) and temperature (solid circles) fluctuations and larval abundance of (b) carp, (c) Australian smelt, (d) redfin perch, (e) carp gudgeons and (f) gambusia, for combined SNE and hand trawl samples during 1999 and 2000 sampling trips. Bar shows total abundance of larvae, solid portion of bar is proportion of protolarvae or PL1 stage for gambusia. ▲ On x-axes indicate sampling trips.

Habitat use

In general, larvae of most species showed no significant habitat change between successive sampling trips within a year (χ^2 test, $P > 0.05$). The only exception was Australian smelt in the 2000 sampling, when its habitat use changed from predominantly using deeper water in the anabranch and billabongs, to also using the floodplain proper habitat during the late October flood (χ^2 test, $P < 0.05$).

Australian smelt, carp gudgeons and redfin perch all showed the same habitat preferences between the two sampling years (Figure 7.7). Carp larvae exhibited a strong change in habitat preference between the two sampling years, with strong positive associations with edge habitats of billabongs in 1999, changing to significant positive association with floodplain proper habitats in 2000 (Figure 7.7a). This is due mainly to the high abundance of carp protolarvae in the floodplain proper during the late October flood (Figure 7.6b). Gambusia also showed a slight change in their habitat preference between the two years, with a significant positive association to the edges of billabong habitats during 1999, while in 2000 utilising both the edges of billabongs and the floodplain proper (Figure 7.7e). Both Australian smelt and carp gudgeons preferred deeper billabong habitats, while redfin perch showed no clear habitat preferences (Figure 7.7 b, c & d).

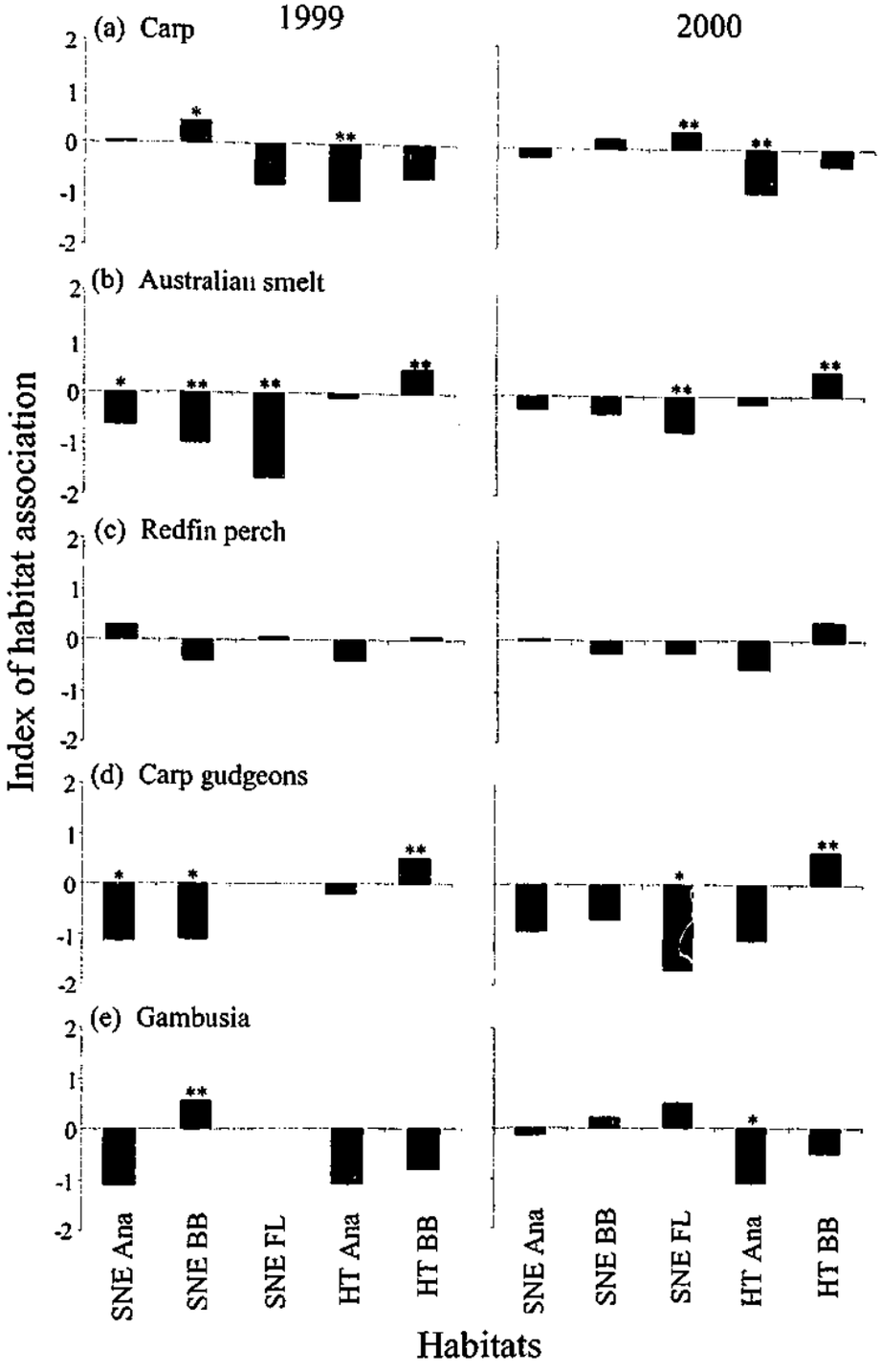


Figure 7.7: Index of habitat association for (a) carp, (b) Australian smelt, (c) redfin perch, (d) carp gudgeons and (e) gambusia for each of the five habitat types during 1999 and 2000. Significance tests based on randomised distributions (see text for details), * = $P < 0.05$, ** = $P < 0.01$. SNE Ana = SNE anabranch (edge habitats of anabranches sampled with SNE method), SNE BB = SNE billabong (edge habitats of billabongs sampled with SNE method), SNE FL = SNE floodplain (floodplain habitats), HT Ana = hand trawl anabranch (surface of deeper water in anabranches sampled with hand trawl method) and HT BB = hand trawl billabong (surface of deeper water in billabongs sampled with hand trawl method).

7.4 Discussion

Occurrence of larvae on the flood plain

Floodplain habitats have been demonstrated to be important nursery areas for larval and juvenile fishes in large floodplain rivers (Welcomme 1985, Finger and Stewart 1987, Turner *et al.* 1994, Killgore and Baker 1996). Some fishes undergo migrations from the main river channel to utilise temporarily inundated habitats for spawning and feeding (Goulding 1980, Ross and Baker 1983, Welcomme 1985, Fernandes 1997, Poizat and Crivelli 1997), while others reside and recruit in a range of permanent and semi-permanent habitats such as off-channel lakes (billabongs) and anabranches (Copp 1989b, Copp *et al.* 1994). Of the 19 fish species known to occur in the Ovens River, the larvae of only five species were collected from the floodplain environment in sufficient numbers to indicate widespread spawning. These included two native taxa, Australian smelt and carp gudgeons, and three introduced species, redfin perch, carp and gambusia. Another five species were collected only rarely in the floodplain environment in 2000. Three of these, Murray jollytail, southern pygmy perch and oriental weatherloach, are typically billabong dwelling species, and were probably only collected due to the connection of previously isolated billabongs.

All five common species occurred as larvae and recruited during both the non-flood and flood years. Each of these species can reside and recruit in the main channel of rivers and in isolated permanent billabong environments (McDowall 1996, Humphries *et al.* in press, Chapter 4). Turner *et al.* (1994) also demonstrated that the larvae found in floodplain habitats of the Tallahatchie River, USA, were from species that reside in both river and permanent floodplain habitats. In addition, two taxa in the present study, carp gudgeons and gambusia, only spawned during low flow conditions in floodplain habitats even in the high flow year. This suggests that these species may have a preference for low flow conditions for spawning and the successful rearing of their young in floodplain habitats, similar to that proposed in the low flow recruitment hypothesis for main channel habitats (Humphries *et al.* 1999).

Despite the perceived importance of flooding in the spawning and recruitment of native fish in the Murray-Darling Basin (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992, Harris and Gehrke 1994, Lloyd *et al.* 1994, Schiller and Harris 2001), only carp, an introduced species, showed an increase in

the abundance of larvae during the major flood event in October 2000. In addition, the peak abundance of total larvae did not occur during flood events, but rather during low flow conditions. The low utilisation of the inundated floodplain environment for fish recruitment demonstrated in this study, fails to support both the findings of a number of previous overseas studies on the importance of the flood plain for fish recruitment (Welcomme 1985, Junk *et al.* 1989), and the proposed 'flood recruitment model' (FRM) for native fish of the Murray-Darling Basin (Harris and Gehrke 1994).

Environmental requirements for the optimum use of the inundated flood plain

The use of the inundated flood plain for fish recruitment is likely to be influenced by a number of interrelated factors, such as the degree of coupling between high flows and temperature, the predicability of the flood pulse, the rate of rise and fall of the hydrograph, the duration of the inundation period and the amount of the flood plain that is inundated (Welcomme 1985, Junk *et al.* 1989, Lloyd *et al.* 1989, Bayley 1991, McKinnon 1997, Sparks *et al.* 1998, Benke *et al.* 2000). Based on these factors, mostly from studies in tropical system overseas, I have developed a model of the likely optimum conditions for use of the inundated flood plain for fish recruitment (Figure 7.8). Each of the factors is discussed here, in terms of the evidence of their importance, applicability and occurrence in the temperate region of the Murray-Darling Basin. The Ovens River is one of the few remaining unregulated rivers in the southern region of the Basin, and it is used here to evaluate the applicability of the environmental requirements for optimum use of the flood plain in the rivers of this region under natural flow conditions.

Fish should spawn at the time of year that maximises the success of production of recruits into the population (Wooton 1998). Generally fishes spawn during the warmest months of the year, partly due to increased growth rates when temperatures are higher and partly because, at least in temperate systems, this is the period of maximum production of food for larvae and juveniles (Jobling 1995). In tropical systems, seasonal changes in temperature and daylength patterns are relatively small, and often the major predictable seasonal event is a rise in water level (Lowe-McConnell 1975, Welcomme 1985). Therefore in these systems, the timing and height of the flood peak cues spawning and movement of adult fish of a range of species onto the flood plain (Welcomme 1985). In temperate systems, the timing of fish spawning is more likely to be controlled by temperature and light regimes than flooding cycles (Wooton 1998, Humphries *et al.* 1999).

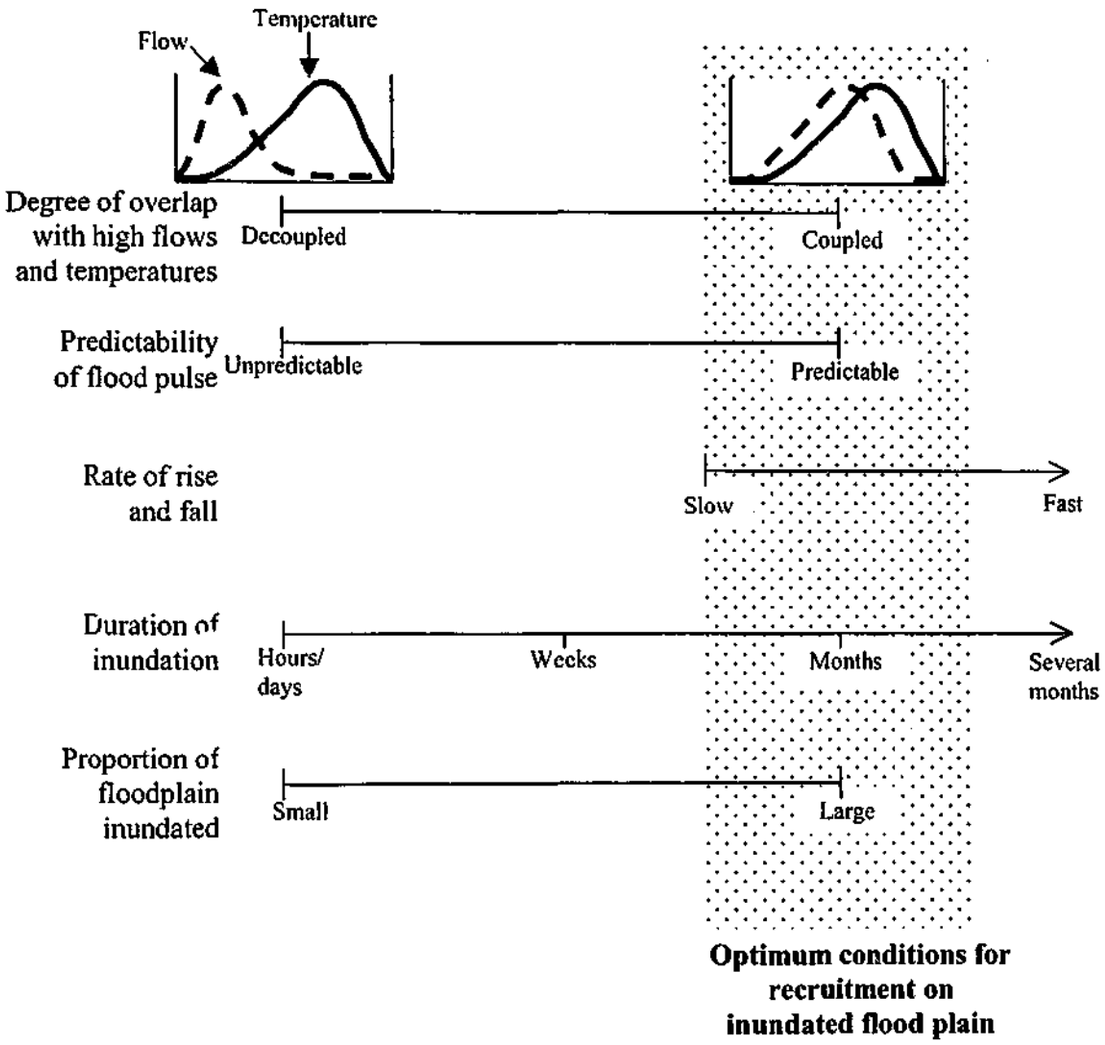


Figure 7.8: Conceptual model of the optimum environmental conditions for utilisation of the inundated flood plain for fish recruitment.

Junk *et al.* (1989), in the 'flood pulse concept' (FPC), therefore emphasised the importance of a 'coupled' rise in flow and temperature in maximising the use of the flood plain for fish recruitment in temperate floodplain rivers, as they provide the best conditions for spawning and successful rearing of their larvae. For example, Finger and Stewart (1987) demonstrated that the timing and duration of flooding in any one year could control the dominance of spring versus summer spawning species in a fish community. Any departure from this condition could result in a disturbance, with a 'decoupling' of high flows and temperature resulting in poor recruitment because of limited nursery areas and a reduction in food supply and/or spawning sites (Junk *et al.* 1989, Sparks *et al.* 1990).

In the Murray-Darling Basin, the relationship between flow and temperature varies throughout the different climatic regions (Humphries *et al.* 1999). In the northern region of the Basin, flooding tends to occur during summer when temperatures are high (Young, 1999, Gehrke 2001), whereas in the southern temperate region, flooding occurs in late winter to early spring, before water temperatures have risen substantially (Young and Hillman 2001). The Ovens River represents a classic example of Junk *et al.*'s 'decoupled' scenario (Figure 7.9a). The highest mean monthly flows occur in spring due to snow melt and heavy rain, whereas the highest water temperatures generally occur a few months later in summer. In 26 out of 100 years, no overbank flows will occur in the Ovens River (Data source: Theiss Environmental Services, Victoria). However, of the remaining years, flooding occurs in spring approximately 50% of the time, but rarely in summer (Figure 7.10a). Although temperature and flow in the Ovens River are 'decoupled', spring spawners could perhaps benefit from the spring flooding. Of the 19 species known to exist in the lowland reaches of the Ovens River, five (mountain galaxias, southern pygmy perch, redfin perch, trout cod, and flyspecked hardyhead) are thought to be solely spring spawners (Figure 7.9b). The remainder either spawn over both the spring and summer period or are solely summer spawners. In the present study, most of the solely spring spawners were not captured in significant numbers during the flood periods, suggesting either patchy or low levels of recruitment or low adult abundance. Redfin perch and Australian smelt occurred in high numbers in both years, but showed no evidence of an increase in spawning or recruitment success with flooding. Carp was the only species to demonstrate any increase in larval abundance during the flood event in late October 2000.

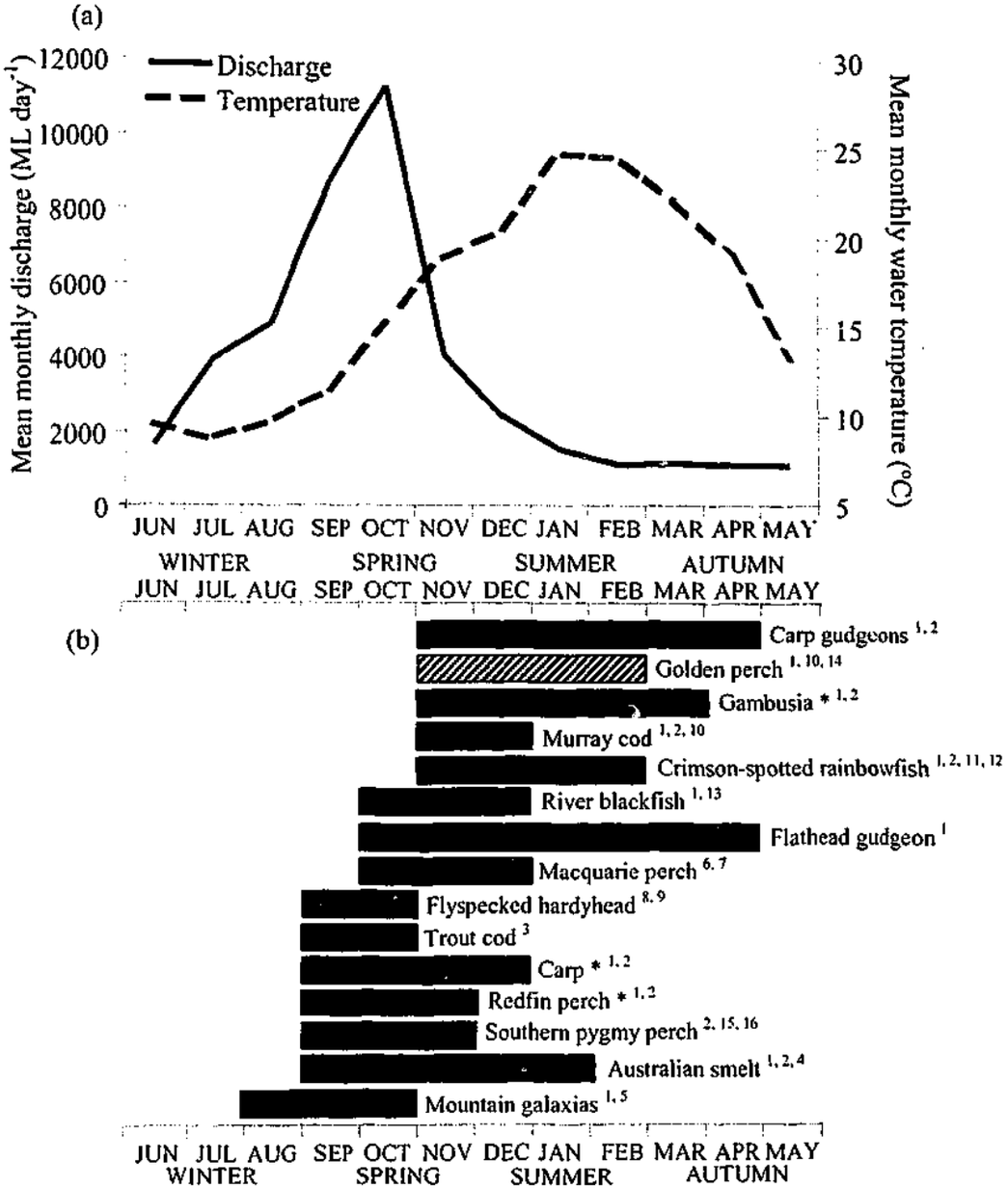


Figure 7.9: (a) Mean monthly discharge and water temperature (°C), and (b) estimated spawning calendar for fish in the Ovens River. Mean monthly data calculated from flow and temperature records at Wangaratta on the Ovens River for 1977 to 1989 (Theiss Environmental Services, Victoria). Currently there is little information about the spawning period of Murray jollytail, silver perch, goldfish and oriental weatherloach, therefore these species are excluded from this Figure. Hatched bar represents potential golden perch spawning period which may be triggered by flooding during this period (Lake 1967a, Mackay 1973). Spawning period for carp gudgeons is a combined period for the three species in the complex. * introduced species. Spawning calendar based on estimates using 1. Humphries *et al.* (in press), 2. This study, 3. Ingram and Douglas (1995), 4. Milton and Arthington (1985), 5. O'Connor and Koehn (1991), 6. Cadwallader and Rogan (1977), 7. Appleford *et al.* (1998), 8. Milton and Arthington (1983), 9. Llewellyn (1979), 10. Cadwallader (1977), 11. Backhouse and Frusher (1980), 12. Milton and Arthington (1984), 13. Jackson (1978), 14. Mackay (1973), 15. Llewellyn (1974), 16. Humphries (1995).

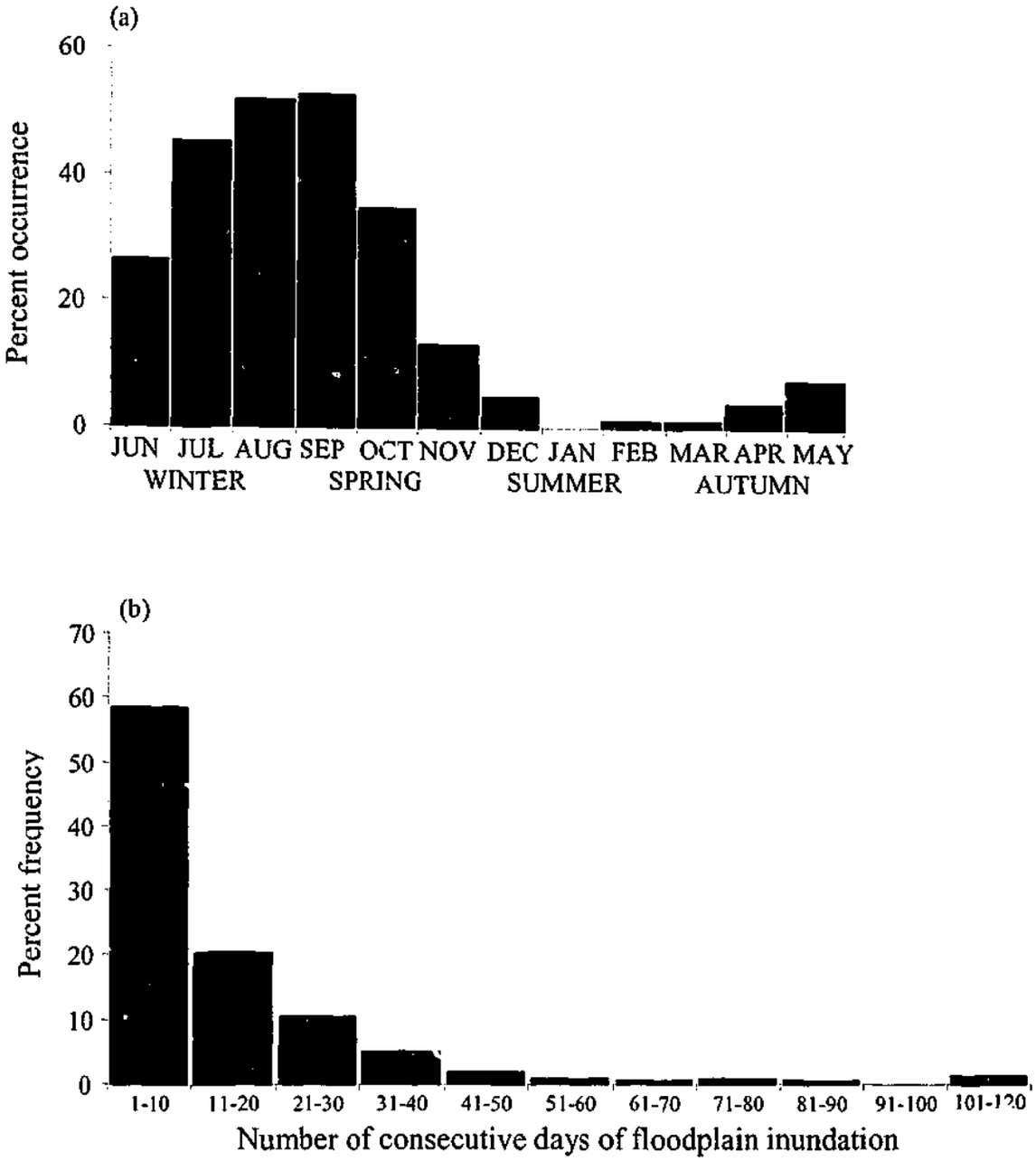


Figure 7.10: (a) Percent occurrence of floodplain inundation (> 15,000 ML day^{-1} at Wangaratta) per month and (b) percent frequency of the number of consecutive days of floodplain inundation in the Ovens River at Wangaratta. Calculated from flow data from 1892 to 1997. Consecutive day calculation of floodplain inundation also includes non-flood periods of less 10 days duration between consecutive flood events.

The FPC was primarily developed from observations on large tropical rivers, where the flood pulse is highly predictable (Junk *et al.* 1989, Junk and Welcomme 1990). The interannual predictability of floods is critical for strong fish recruitment and production in large rivers and favours the development of morphological, anatomical, behavioural and physiological adaptations of aquatic organisms to flooding (Junk *et al.* 1989, Bayley 1991). Rivers of the Murray-Darling Basin are well known to have high interannual variability (Walker 1992, Walker *et al.* 1995, Puckridge *et al.* 1998). In an analysis of the hydrological characteristics of a number of the world's rivers, the dryland rivers of the Murray-Darling Basin and tropical rivers were found to be at the extreme opposite ends of a continuum of hydrological variability (Puckridge *et al.* 1998). Puckridge *et al.* (1998) also suggested that dryland rivers such as the Cooper and Diamantina Creeks in the northern region of the Basin, could be considered to be of the most variable in the world. However, unpredictability does not necessarily preclude the development of adaptations to flow, since opportunism, flexibility and trophic generalisation could be viewed as evolutionary adaptations to a variable flow regime (Poff and Alan 1995, Walker *et al.* 1995, Puckridge *et al.* 1998).

The rate of change from one flow condition to another can influence the range and strength of biotic responses to flooding (Poff *et al.* 1997). A slow to moderate increase in water level is likely to produce strong year classes, since fish are thought to respond to the increased production of vegetation and associated food and habitat as the moving littoral zone traverses the flood plain (Welcomme 1979, Junk *et al.* 1989, Bayley 1991). A slow rate of rise is characteristic of a smooth hydrograph, where floodwaters are maintained for a long duration, whereas a rapid rise (or fall) is characteristic of systems with fast drainage rates. In some systems, a rapid rise in water level may be followed by a rapid fall, and therefore, the flood may have little direct benefit for aquatic biota (Bayley 1991). In cases where sudden changes in the hydrograph occur, fish may be displaced downstream during sudden rises or they may be left stranded in isolated pools on the flood plain during the drying phase (Bonetto *et al.* 1969, Lowe-McConnell 1975, Welcomme 1985, Lloyd *et al.* 1989, Pearsons *et al.* 1992). Bonetto *et al.* (1969) estimated that 40,000 tonnes of fish are lost via stranding in the Parana River system every year. In the present study, large numbers of carp larvae and juveniles were left stranded in temporary, shallow pools on the flood plain after the major flood event in October 2000 (pers. obs). Poizat and Crivelli

(1997) also observed stranding of some species, including carp, when water levels fell in a seasonally flooded wetland.

The length of time floodwaters remain on the flood plain can also dictate the strength of biotic responses to the flood (Halyk and Balon 1983, Junk *et al.* 1989, Boulton and Lloyd 1992, Poff *et al.* 1997). However, constant high water levels can also create areas on the flood plain with poor water quality and can reduce fish production (Junk *et al.* 1989). A number of studies have suggested that varying periods of inundation are critical for the optimum use of the flood plain for fish recruitment. At one end of the extreme, floodplain inundation in tropical regions commonly occurs for periods of up to six months (Goulding 1980, Welcomme 1985). In the Mississippi River, Sparks *et al.* (1998) demonstrated that long (six weeks or more), slowly receding floods were critically important for utilisation of the flood plain by fishes, especially for those species which build nests. In Australia, no studies have demonstrated the period required for successful utilisation of the flood plain for fish recruitment. However, suggested values based on the estimated time between spawning and development into juveniles of some native fishes, have ranged from two to four months (Geddes and Puckridge 1988, Lloyd *et al.* 1989, McKinnon 1997). McKinnon (1997) recommended that manipulated floodplain inundation in Barmah Forest on the Murray River should last for at least four months to have tangible benefits to native fish. He suggested that this extended period allowed for the detection of flooding by riverine species, migration of adults into the forest from the river, sexual maturation of adult fish, growth and recruitment of their young, and finally, the return of adult and juvenile fish from the flood plain.

In the Ovens River, nearly 60% of floods will occur for less than ten consecutive days, while floods of more than 40 days duration are very rare (Figure 7.10b). A similar pattern of flood duration periods is likely to have occurred for most rivers of similar size in the southern winter rainfall region of the Basin prior to river regulation. In these systems, fish may risk becoming stranded if they utilise the flood plain for recruitment, especially if they have specialised spawning requirements or lengthy larval development periods, such as Murray cod, trout cod and river blackfish (Humphries *et al.* 1999).

The amount of the flood plain under inundation is also thought to influence the number of fish produced from the flood plain (Welcomme 1985, Bayley 1991), mainly by influencing

the diversity of aquatic habitats available for spawning and rearing of their young. This was demonstrated by Killgore and Baker (1996), who found that higher catches of larval fish corresponded with higher water levels that expanded the aquatic-terrestrial transition zone and increased production within the forested flood plain. Whilst the amount of flood plain under inundation at any particular discharge is not currently known for the Ovens River, the area inundated is likely to have decreased from natural conditions due to levee banks in the lowland reaches of the River (Cottingham *et al.* 2001b).

Benke *et al.* (2000) argues that ecologists need to understand the inundation patterns within a system to be able to quantify the importance of the flood pulse. The exploration of the environmental conditions required for optimum use of the flood plain for fish recruitment presented here, has demonstrated that most of these conditions rarely occur in the Ovens River catchment, particularly the low incidence of coupling of high flows and temperatures and long periods of floodplain inundation. This is likely to also be true for other rivers in the southern winter rainfall region of the Murray-Darling Basin, especially under their natural flooding regimes.

Life history characteristics, floodplain fish recruitment and the Ovens River

For a fish species to successfully utilise the floodplain for recruitment, specific adaptations or life history characteristics suited to this unpredictable and fluctuating environment are probably required. These include adaptations to poor water quality, protracted or flexible spawning period, a drifting larval phase, generalist spawning habitat requirements, longevity and rapid larval development. The fish fauna of the Ovens River demonstrate a variety of adaptations that may or may not allow them to take advantage of inundated floodplain environments (Table 7.5).

For a species to utilise the inundated floodplain for recruitment, it is critical that its natural spawning period occurs during the potential flood period. In the Ovens River, flooding generally occurs in late winter and early spring (Figure 7.9a and 7.10a). Most species that occur in the river can spawn during this period (Figure 7.9b). For summer spawning species, such as Murray cod, golden and silver perch, carp gudgeons and gambusia, there is a much lower chance of flooding occurring during their spawning period (Figure 7.9 and

Table 7.5: An assessment of the likelihood of the fish fauna in the Ovens River to use inundated flood plains for recruitment based on advantageous life history characteristics. Y = yes, N = No, ? = no information or estimate, * = introduced species, LB = live bearers. Overlapping spawning periods: based on Figure 7.8; Flexible or protracted spawning period: Humphries *et al.* (in press) and estimates based on review in Koehn and O'Connor (1990b); Generalist spawning attachments: includes broadcast and pelagic spawners, based on McDowall (1996); Larval drift: Humphries *et al.* (in press), and this study; Rapid development: estimate of spawning to juvenile period, this category is based mostly on estimates from Lake (1967b), Vilizzi (1998b) and P. Humphries (pers. comm.); Adaptations to poor water quality: golden and silver perch (Gehrke 1991), gambusia, carp and oriental weatherloach (D. McNeil, pers. comm.); Longevity: McDowall (1996).

	Golden perch	Silver perch	Macquarie perch	River blackfish	Murray cod	Trout cod	Rainbowfish	Carp gudgeons	Southern pygmy perch	Mountain galaxias	Murray jollytail	Australian smelt	Flathead gudgeon	Flyspecked hardyhead	Gambusia *	Carp *	Goldfish *	Redfin perch *	Oriental weatherloach *
Overlapping spawning and flood period in Ovens River	N?	?	Y	Y	N	Y	N	N	Y	Y	?	Y	Y	Y	N	Y	Y?	Y	?
Flexible spawning period	Y	Y?	N	N	N	N	N	N	N	N	?	N	N	N	Y (multiple broods)	Y (multiple spawning)	N	N	?
Protracted spawning period	N	N	N	N	N	N	N	N	N	N	?	Y	Y	N	N	N	N	N	?
Generalist spawning attachments	Y	Y	N	N	N	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Larval drift	Y?	Y?	Y?	N	Y	Y	N	N	N	N	N	Y	Y	N	N	Y	Y?	N	N
Rapid development (spawning to juvenile period)	Y (21 d)	Y (21 d)	Y? (21 d)	N? (30 d)	N (36 d)	N? (36 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y? (14 d)	Y (LB)	Y (20 d)	Y? (20 d)	N (60 d)	?
Adaptations to poor water quality	N	N	?	?	?	?	?	?	?	?	?	?	?	?	Y	Y	Y?	?	Y
Longevity (> 3 years)	Y	Y	Y	Y	Y	Y	N	N	N	N	N	N	N	N	N	Y	Y	Y	Y
Likelihood of use of floodplain for fish recruitment	**LOW**	**LOW**	**MED**	**LOW**	**MED**	**MED**	**LOW**	**LOW**	**LOW**	**LOW**	**LOW**	**MED**	**MED**	**LOW**	**MED**	**HIGH**	**MED**	**MED**	**LOW**

7.10a). A flexible spawning period, that allows a species to delay its spawning until the right conditions are present, for example a flood, may provide enhanced recruitment success. Golden perch and possibly silver perch are thought to spawn only when water levels rise after a critical minimum water temperature of 23°C has been reached (Lake 1967a, Mackay 1973). Protracted spawning may also potentially allow at least a proportion of the young to encounter flood periods. In the Ovens River, only two species, Australian smelt and flathead gudgeon are thought to have protracted spawning periods (Table 7.5).

When flooding does occur in the Ovens River it rarely remains inundated for more than 10 days. Therefore, characteristics such as generalist spawning habitat requirements (such as broadcast and pelagic spawning) and rapid development of young may be an advantage. Species with specialist spawning requirements such as nest building, parental care, or those with slow egg and larval development periods, could risk stranding if they utilise flood plains and the inundation period does not last long enough to complete the rearing of young. In tropical floodplain rivers, nest building among fishes is very common (Welcomme 1985). However, in tropical systems the inundation period is much longer, in the order of months, rather than days as in the Ovens River. Of the fish species in the Ovens River, river blackfish, Murray cod and trout cod, all have long developmental periods and exhibit some parental care of their eggs and/or larvae (Table 7.5). Therefore, these species would risk stranding if they utilised floodplain environments as spawning or nursery sites.

Recruitment in the inundated floodplain environment is commonly thought to occur via two main mechanisms: either adult fish move onto the flood plain and spawn in inundated floodplain areas; or their larvae and/or juveniles drift from the main channel into the inundated floodplain (Geddes and Puckridge 1988, Harris & Gehrke 1994, Schiller and Harris 2001). In tropical regions, adult fish of a number of species move onto the flood plain during the extended flood periods, both to spawn and feed on the variety of food sources available (Welcomme 1985, Goulding 1980). Studies in temperate regions have also observed movements of adults onto the floodplain during inundation, and suggest that this may be linked to spawning movements (Ross and Baker 1983, Fernandes 1997). Although a number of species in the Murray-Darling Basin can undergo large longitudinal migrations (Reynolds 1983, Koehn 1986, 1997), adult movements laterally onto the flood

plain are generally assumed to be possible, but are so far largely undocumented (Humphries *et al.* 1999). Whilst true lateral movements of larval and juvenile fish into floodplain environments have not been studied, species such as Murray cod and carp are known to drift in main channel environments (Humphries *et al.* in press, Chapter 4). Golden and silver perch are also thought to have drifting egg and larval stages (Lake 1967 a & b), but as yet have not been collected in large numbers in the wild. This drifting strategy may allow eggs or larvae originating from the main channel to drift onto the inundated floodplain.

Inundated floodplain environments often experience poor water quality conditions, especially low dissolved oxygen levels and high concentrations of tannins and polyphenols (Welcomme 1985, Junk *et al.* 1989, McKinnon 1997, Fontenot *et al.* 2001). Thus, it would be advantageous for fishes in this environment to be able to avoid or tolerate adverse water quality conditions. Air breathing and other adaptations to low oxygen concentrations are frequently found in tropical floodplain fishes (Welcomme 1979, Welcomme 1985, Junk *et al.* 1989). Gehrke (1990a, 1991), in a series of experiments, demonstrated that golden and silver perch larvae avoided areas where dissolved oxygen concentrations were low in an artificial floodplain environment. Further, whilst golden perch larvae may be attracted to floodplain environments via river red gum leachate (Gehrke 1990b), high concentrations of the leachate can be lethal (Gehrke *et al.* 1993). However, four of the five introduced species in the Ovens River exhibit adaptations to poor water quality (Table 7.5) including air or surface breathing (Odum and Caldwell 1955, Lewis 1970, Ott *et al.* 1980, Koehn *et al.* 2000, D. McNeil, LaTrobe University, pers. comm.).

Finally, the frequency of flooding influences the capacity of a population to respond to flooding, and this will vary with the generation times of each species (Walker *et al.* 1995). For example, if flooding occurs irregularly, short-lived species may not live long enough to encounter suitable periods of floodplain inundation. Thus, longevity may be an advantageous life history trait for flood-dependent species, especially in systems with a low frequency of flooding.

Most species of fish in the Ovens River exhibit only a few of the characteristics that may be advantageous for utilising inundated floodplains for recruitment, and are therefore rated as either "low" or "medium" likelihood to utilise the flood plain for recruitment (Table

7.5). Most of these species were not found as larvae in the present study. Some species which were rated as either "low" or "medium" such as redfin, carp gudgeons, Australian smelt, and gambusia, were found to spawn and recruit on the flood plain during both non-flood and flood years, suggesting that for these species flooding is not critical to either initiate spawning or for successful recruitment. Interestingly, carp gudgeons and gambusia, seemed to delay their spawning in the high flow year until after the flood period had passed, perhaps indicating an association between low flow conditions and successful rearing of their young.

Golden and silver perch exhibit a number of the life history characteristics favourable for utilisation of the inundated flood plain, such as flexible spawning period, drifting larvae, and rapid development of their eggs and larvae (Table 7.5). However, they received an overall rating of only "low" likelihood to utilise the inundated flood plain in the Ovens River, primarily because flooding rarely occurs when the suggested critical spawning temperature of 23 °C is reached (Figure 7.9). Aquaculture studies in the early 1960's, suggested that golden perch require a rise in water level above a critical temperature threshold to initiate spawning (Lake 1967a). Mackay (1973) also suggested that golden perch spawning is linked to flooding and that poor recruitment occurs in low flow years. However, in contrast, strong year classes of golden and silver perch were associated with years of within channel spring flows rather than flood years in the Murray River (Mallen-Cooper *et al.* 1995).

To date, the only known collection of golden perch larvae in the wild is of a few individuals from the Broken River during a low flow period (Humphries *et al.* in press). Although abundant as adults in the river, the larvae of golden perch were not found in the present study, presumably because flooding did not coincide with their potential breeding period (Figure 7.9). Therefore in the southern region of the Basin, where floods generally occur throughout the winter/spring period, the likelihood of successful recruitment of golden perch is greatly reduced. In contrast, the northern region of the Basin receives flooding in summer that is of a long duration (Humphries *et al.* 1999, Young 1999). The main factors controlling the use of the flood plain for fish recruitment in these environments, is likely to be the unpredictability and low incidence of flooding. However, golden perch exhibit some possible adaptations to this unpredictability, such as flexibility in spawning and longevity (Walker *et al.* 1995, McDowall 1996). In recent years, juvenile

golden perch have been found during extensive periods of flooding in the northern region of the Basin (S. Bunn, Griffith University, pers. comm.), although the exact cue for spawning and background level of recruitment during low flow years has not been established.

Carp have a number of characteristics that allow them to take advantage of unpredictable flood conditions (Table 7.5), and were the only species in the present study to demonstrate an increase in larval abundance with the major flood event in October 2000. Koehn *et al.* (2000) suggested that there is anecdotal evidence to suggest that individual female carp do not deposit all their eggs at once, potentially allowing an individual to spawn a number of times over one spawning season. In the present study, a second spawning event, evidenced by a high proportion of newly hatched carp larvae, occurred on the flood event in October 2000. However, this may indicate either repeated spawning of individuals or a delay in spawning of some individuals within the population. McKinnon (1997) also observed multiple spawning events of carp in Barmah Forest on the Murray River during extended periods of inundation. The preferred spawning habitat for carp is usually on dense macrophytes, but they can also spawn on live or dead terrestrial grasses or river red gum branches (Panek 1987, Koehn *et al.* 2000), all of which are abundant in floodplain environments. Recent radiotracking studies in the Murray River have suggested that adult carp move onto flood plains during periods of inundation to spawn on the newly flooded vegetation (I. Stuart, Department of Natural Resources Environment Victoria, pers. comm.). Additionally, newly hatched carp larvae were found in the present study to both drift onto the inundated flood plain from the main channel and were also abundant on the floodplain proper. This suggests that colonisation of the flood plain by carp larvae probably occurred via both drifting larvae from the main channel and adult spawning on the floodplain proper.

Concluding remarks

Despite the lack of clear supporting evidence, the importance of the flood plain for fish recruitment in the Murray-Darling Basin has been commonly extrapolated to all regions of the Basin and sometimes even to all native species within the Basin (Geddes and Puckridge 1988, Lloyd *et al.* 1989, Harris and Gehrke 1994, Lloyd *et al.* 1994, Schiller and Harris 2001). This study has demonstrated that for at least the rivers in the winter rainfall region of the Basin, such as the Ovens River, the conditions required for optimum use of the flood

plain for fish recruitment rarely occur. The only species that appears to be flexible enough in its life history to successfully utilise the inundated flood plain for recruitment in most years is carp. However, even carp are also capable of spawning and recruiting in low flow conditions on the flood plain and also within the main channel environment. Golden perch also display a number of the suggested life history characteristics required for utilisation of the flood plain for fish recruitment. However, they are unlikely to use the flood plain in the winter rainfall region of the Basin, but may recruit well during flood years in the north of the Basin, where the timing of floods and high temperatures are often coupled.

This study has demonstrated that the optimum environmental conditions and life history adaptations for direct use of the flood plain for fish recruitment do not necessarily occur in all floodplain rivers or for all fish species present in them. It is proposed that the use of the flood plain for fish recruitment is governed by a number of factors such as the coupling of high flows and temperatures, predictability of the flood pulse, the duration of the inundation period and the variety and occurrence of advantageous life history characteristics of the river's fish fauna.

However, we are still a long way from conclusively defining the role of the flood plain in fish community dynamics. In systems where the use of the floodplain environment for spawning and recruitment is limited, periods of floodplain inundation may provide valuable indirect benefits to fish recruitment, such as providing a boost of nutrients and zooplankton in returning waters to permanent water bodies, and therefore potentially enhancing recruitment of main channel dwelling species. Flooding also sustains and resets billabong communities, which is of obvious importance to the ecology of wetland dwelling species. Finally, this study has only examined the role of overbank flows, i.e. the 'flood pulse', and did not examine the role of within channel rises, i.e. the 'flow-pulse', (*sensu* Puckridge *et al.* 1998; Tockner *et al.* 2000) on fish recruitment dynamics. Further work is required to elucidate the importance of other roles flooding and flow-pulses may have in the ecology of fishes in floodplain rivers.

Chapter 8: General Discussion

The broad aim of this thesis was to examine a number of the previously untested assumptions of both the 'flood recruitment model' (FRM) (Harris and Gehrke 1994) and the 'low flow recruitment hypothesis' (LFRH) (Humphries *et al.* 1999) for fish in floodplain rivers of the Murray-Darling Basin. Although these two models were based on observations and studies in the Basin, their applicability is not restricted to the Murray-Darling Basin alone. This study constituted the first attempt at empirically testing the LFRH. Additionally, this study tested the applicability of the FRM for the Murray-Darling Basin, and the predictions for fish recruitment in temperate regions proposed in the 'flood pulse concept' (FPC) (Junk *et al.* 1989).

A central aspect of the FRM is the assumption that the main channel of floodplain rivers does not support high enough densities of adequately sized zooplankton to sustain larval fish, and that the only environment where the required densities do occur is on the inundated floodplain (Lake 1967a, Arumugam and Geddes 1987, Geddes and Puckridge 1988, Lloyd *et al.* 1989, Rowland 1992, Harris and Gehrke 1994). In comparison, this study concurs with recent studies (Humphries and Lake 2000, Humphries *et al.* in press), in demonstrating that a number of species can successfully spawn and recruit in the main channel, without flooding or access to the floodplain environment (Chapter 4). Indeed, this study established that an abundant prey source for larval fish does exist in the main channel environment, without inputs from the inundated floodplain (Chapter 6). This prey source was found predominantly in the epibenthic zone, where the density of meiofauna was found to be on average 100 times denser than in the pelagic zone. Traditionally, the densities of zooplankton in the main channel of rivers have been sampled in the pelagic zone only, thereby significantly underestimating the total density and diversity of fauna in these environments. Future studies of meiofauna should include efforts to sample fauna associated with the epibenthic zone and other available surfaces, such as woody debris and macrophytes.

This study demonstrated that the developmental stages of most species consumed a wide variety of prey from the epibenthic, pelagic and surface zones of the water column (Chapter 5). Additionally, the first feeding larvae of some species (eg. Murray cod) did not

necessarily require small prey items, and those species that did (eg. Australian smelt and rainbowfish), soon altered their diets as older larvae to feed on a variety of larger prey items.

The LFRH predicts that recruitment of some species could occur in the main channel of floodplain rivers during low flow periods, by the utilisation of still, warm and shallow littoral and backwater habitats (Humphries *et al.* 1999). The present study supports this prediction (Chapter 4). Backwaters and still littoral areas were important habitats for gambusia and rainbowfish throughout ontogeny, whilst carp and Australian smelt only used them as nursery habitats, undergoing a significant ontogenetic shift in habitat use as juveniles and adults.

The LFRH also proposes that still littoral and backwater habitats can have high densities of potential prey for larval fish relative to other main channel habitats (Humphries *et al.* 1999). However, despite the use of these habitats by larvae (Chapter 4) and high densities of potential prey occurring in the main channel during low flow conditions (Chapter 6), there was little relationship between the densities of prey and the habitat use of the fish larvae. The mechanism behind the use of these nursery habitats requires further investigation and experimental manipulation.

The inundation of the flood plain has been viewed as important, if not critical, for the recruitment of native fishes of the Murray-Darling Basin (Geddes and Puckridge 1988, Lloyd *et al.* 1989, Lloyd *et al.* 1994, Schiller and Harris 2001). However, prior to the current study, the FRM had not been adequately tested, though its generality has been questioned (Humphries *et al.* 1999). In the current study, only five of the 19 fish species known to occur in the non-regulated Ovens River were collected as larvae and recruited on the flood plain. However, all five of these species occurred as larvae and recruited during both non-flood and flood conditions (Chapter 7). The introduced carp was the only species found to demonstrate an increase in larval abundance during flood conditions.

This study demonstrated that both the environmental conditions and life history adaptations for direct use of the flood plain for recruitment do not necessarily occur in all floodplain rivers or for all species present in them (Chapter 7). Rather, the use of the flood plain for recruitment is governed by a number of factors, such as the coupling of high

flows and temperatures, the predictability of the flood pulse, the duration of the inundation period and the occurrence of advantageous life history characteristics of the river's fish fauna. The results of the study suggest that the conditions required for optimum use of the flood plain for recruitment rarely occur in the southern winter rainfall region of the Basin, and that the number of species that utilise the inundated flood plain for recruitment in this region is also likely to be small.

Although the FRM emphasises the direct utilisation of the inundated floodplain by fish larvae to enhance recruitment (Harris and Gehrke 1994, Schiller and Harris 2001), flooding may also provide critical indirect benefits to fish recruitment in the main channel by providing a boost of nutrients and prey in the returning flood waters (Junk *et al.* 1989). This study did not examine these potential indirect benefits of flooding, or the role of in-channel 'flow-pulses' (*sensu* Puckridge *et al.* 1998, Tockner *et al.* 2000), in successful fish recruitment in the main channel environment. However, the studies of the main channel presented in this thesis have emphasised the importance of the trophic link between epibenthic meiofauna and larval fish. These findings lend some support to the predictions of the 'riverine productivity model', which proposes that the major source of organic matter assimilated by animals in large rivers is derived from local autochthonous production (including phytoplankton and benthic algae) or directly from the riparian zone (Thorp and Delong 1994). Whilst the current studies provide information regarding food webs within the main channel, further research is required to assess the importance of indirect benefits of flooding, in-channel flow-pulses and the role of *in-situ* benthic production of organic matter in the ecology of floodplain rivers.

Concluding remarks – a conceptual model of fish recruitment in floodplain rivers

This study demonstrates that the two previous recruitment models proposed for the Basin only partially explain the recruitment strategies of the fish fauna of the Murray-Darling Basin. Based on the findings of the present study and a longer-term study of larval fish (Humphries *et al.* in press), a more generalised conceptual model of recruitment strategies for fish in floodplain rivers is proposed that incorporates both high and low flow conditions (Figure 8.1). For the purposes of this model, recruitment is regarded as the transition from egg to larvae and into the juvenile population, and is not related to the strength of year classes. The model proposes five recruitment strategies, these are:

1. Generalists: Species that are able to spawn and recruit during both high and low flow conditions, in flood plain or main channel habitats. For example, Australian smelt and redfin perch.
2. Flood opportunists: Species that are able to spawn and recruit during both high and low flow conditions, in flood plain or main channel habitats (generalists), but their recruitment is enhanced during flood conditions. For example, carp.
3. Low flow specialists: Species that only spawn and recruit during low flow periods either in flood plain and/or main channel habitats. This is an extension of the strategy proposed in the LFRH into both main channel and floodplain habitats. For example, rainbowfish, carp gudgeons and gambusia.
4. Main channel specialists: Species that only spawn and recruit within the main channel environment, but can do so during either high or low flow events. For example, Murray cod, river blackfish and Mountain galaxiid.
5. Floodplain specialists: Species that only recruit during periods of floodplain inundation. This is based on both the predictions in the FRM and the FPC. For example, golden perch and silver perch.

Supporting evidence for the fifth strategy is at present limited to aquaculture spawning trials (Lake 1967a), observations (Cadwallader 1977) and gonad maturation studies of spawning adults during rises in water level or flood conditions (Mackay 1973). As yet, no larvae of these species have been captured and reported during flood conditions, in any part of the Basin, including during the present study. However, in recent years, researchers working in the northern summer rainfall region of the Basin have captured juvenile golden perch on inundated floodplains (S. Thoms, Griffith University, pers. comm.), although the exact spawning cue and the background level of recruitment during low flow years has not been established.

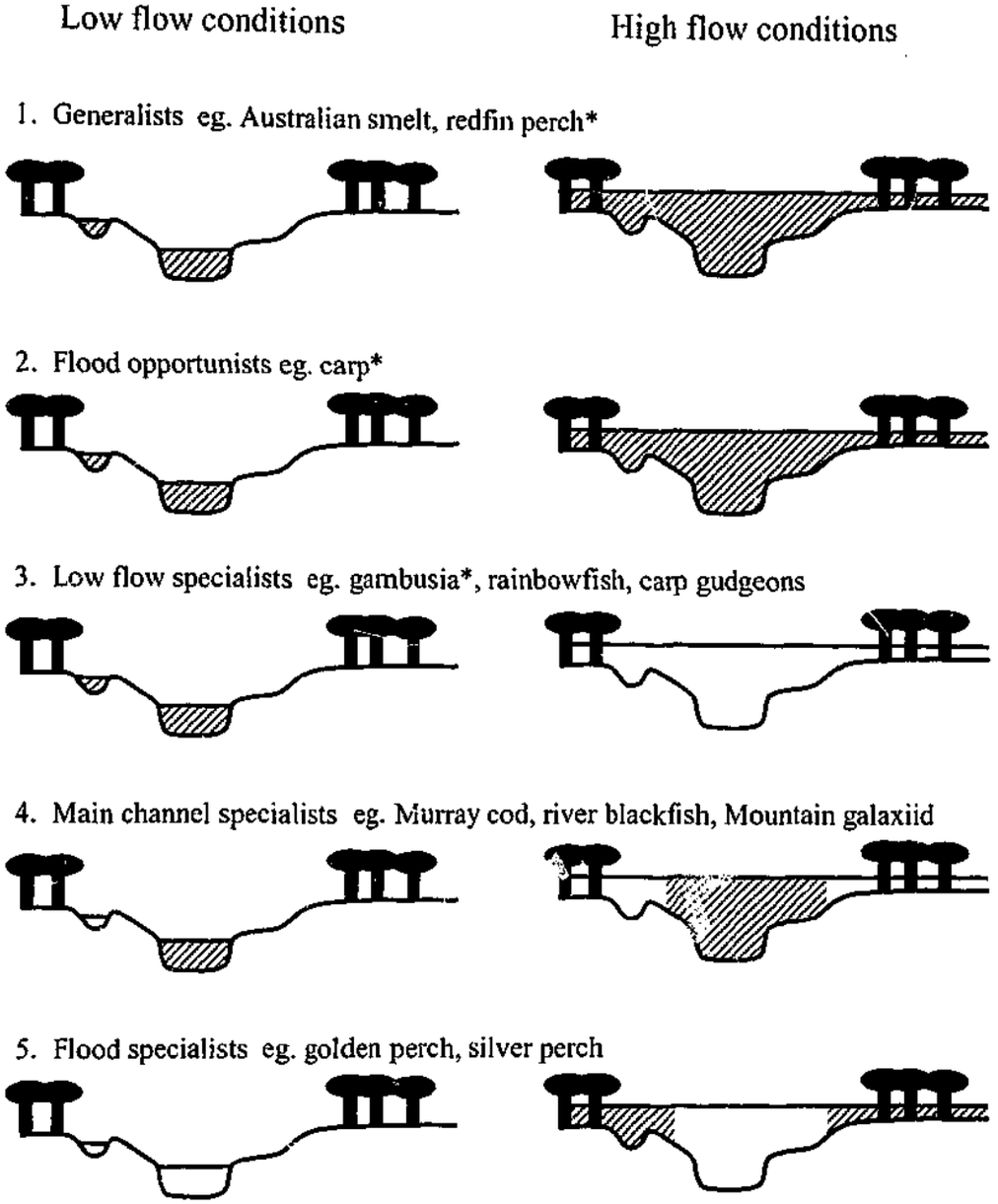


Figure 8.1: Conceptual model of proposed recruitment strategies for fish in floodplain rivers. Hatched areas indicate where recruitment occurs. See text for explanation of recruitment strategies. * = introduced species.

Whilst the proposed model of recruitment strategies for fish in floodplain rivers (Figure 8.1) has been principally derived for fish of the winter rainfall region of the Murray-Darling Basin, and these fish are used as examples in the model, the strategies could also be applied to the fish fauna of other temperate floodplain rivers. The five recruitment strategies proposed in this model are based on the habitat and flow requirements for spawning and recruitment of the fish. The proposed model also includes two strategies; low flow specialists and flood specialists, which are similar to those described in the LFRH and the FRM. The proposed model emphasises the importance of the entire hydrological cycle and both the main channel and floodplain environments in the recruitment of riverine fishes, but importantly it does not preclude the potential role of indirect benefits of flooding or in-channel flow pulses in the ecology of riverine fishes.

Main channel habitats such as backwaters and still littoral areas, are often reduced in abundance and diversity in regulated rivers (Moore and Gregory 1988b, Wintersberger 1996, Winkler *et al.* 1997). This is primarily caused by the scouring and filling of these habitats during constant flows and the flooding of the habitats during the spawning season. However, despite their established importance and degraded nature, backwater and still littoral habitats are often neglected in restoration efforts in rivers (except see Langler and Smith 2001). Currently, most efforts to restore instream habitat in rivers are focussed on restoring adult fish habitat, especially large-scale features, such as pools and large woody debris (eg. White 1996, Cederholm *et al.* 1997, Nicol *et al.* 2001). Restoration efforts for larval fish could include the construction of backwaters and embayments, as demonstrated successfully by Langler and Smith (2001), or restoring the variability of flows to regulated lowland rivers to enable natural channel forming processes to occur (Copp 1992b, Stanford *et al.* 1996).

In conclusion, it is now widely accepted that the environmental effects of river regulation have severely affected the ecological integrity of many of the world's rivers (Ward and Stanford 1979, Dynesius and Nilsson 1994). Increasingly, the management of regulated rivers is including the restoration of components of the natural flow regime to restore ecological functions (eg. Whittington and Hillman 1999). Conceptual models describing ecological processes in rivers are essential for the development of river management strategies (Boulton and Brock 1999, Ward *et al.* 2001). This thesis has provided insight into the processes that influence fish recruitment in temperate floodplain rivers, and has

proposed a conceptual framework for fish recruitment based on empirical data. The studies described in the thesis have demonstrated that previous models used to characterise fish recruitment in floodplain rivers may not be adequate to explain the requirements for all species, under all environmental conditions. This suggests that our understanding of the processes that structure riverine communities should be based on conceptual models that recognise the inherent geographical, climatic and biological variability within and between ecological systems.

Appendix A: Photographs of Larval Stages of Common Species Captured During the Studies Presented in this Thesis.

Photos courtesy of P. Humphries and L. Serafini, unpub. data. White bar on figures shows 1mm.

(a) Carp

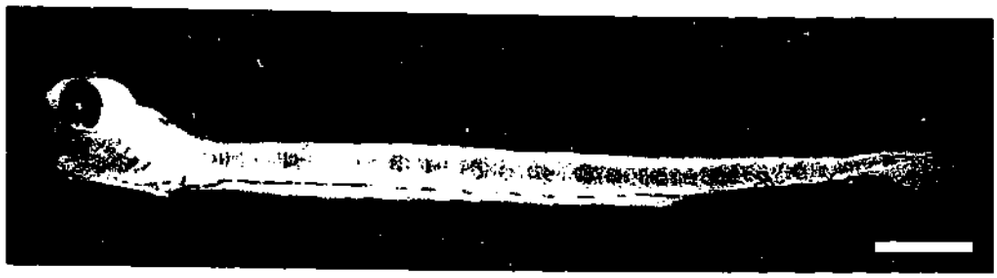
Protolarva

Post Flexion

Metalarva

(b) Australian smelt

Protolarva

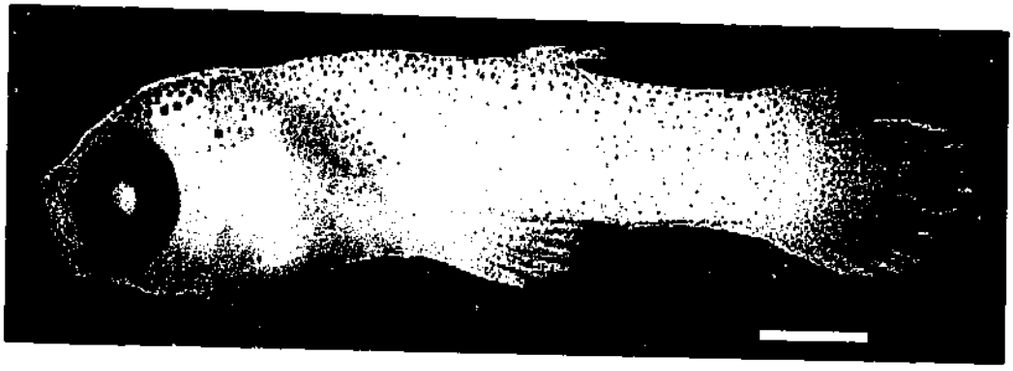


Postflexion

Metalarva

(c) Gambusia

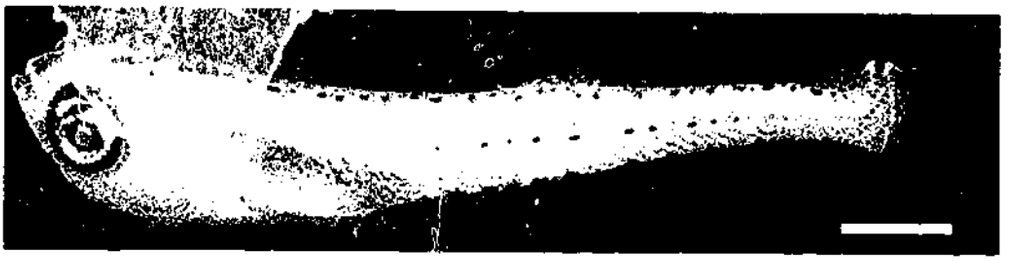
Postlarvae 2



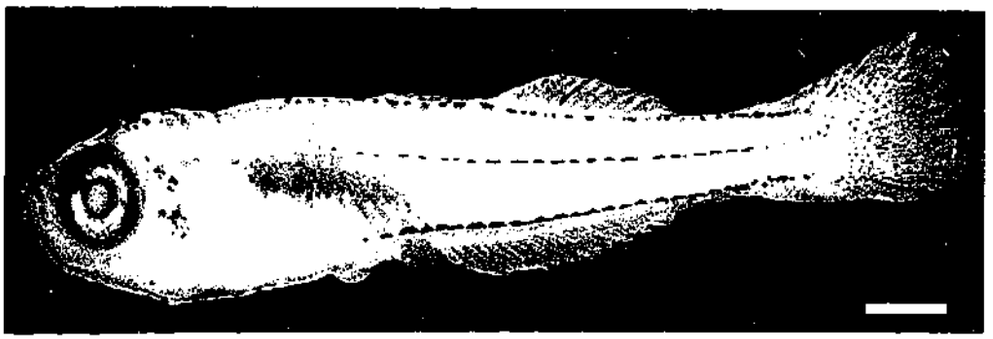
(d) Crimson-spotted rainbowfish

Protolarva

Postf[illegible]

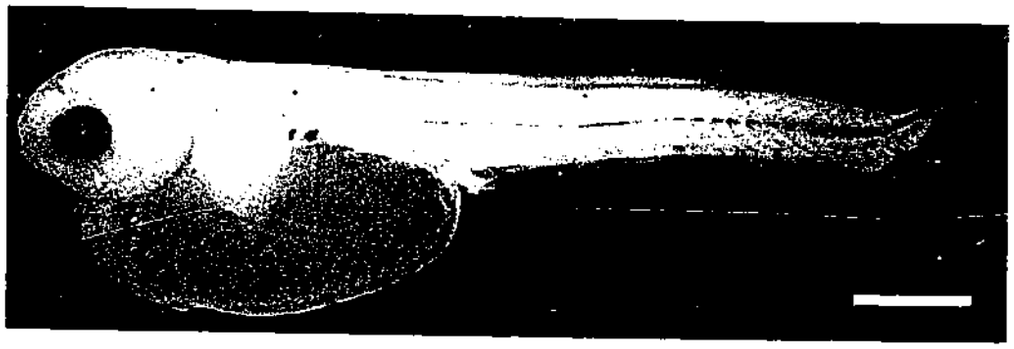


Metalarva

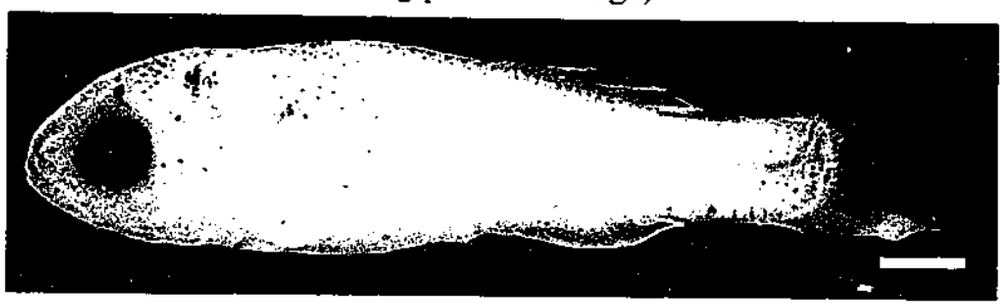


(e) Murray cod

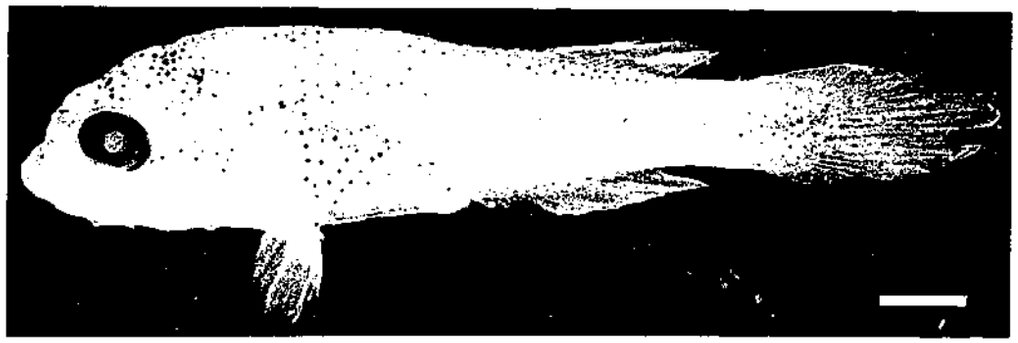
Flexion - day 3



Postflexion - day 12 (drifting postlarval stage)

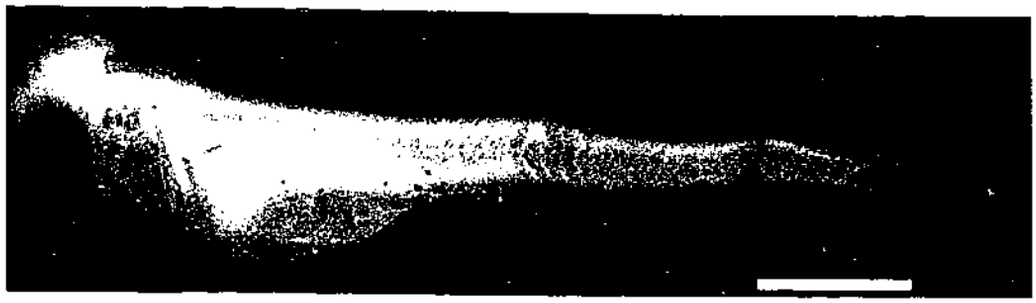


Metalarva - day 18 (settlement juvenile stage)



(f) Redfin perch

Protolarva



Postflexion

Metalarva

Appendix B: Full List of Dietary Items Found in Gut Analysis of all Developmental Stages and Species.

% F = Percent frequency of occurrence, % V = Percent volume contribution.

(a) Carp

Developmental stage		PR		PF		M		JA	
No. Fish		21		60		30		41	
		% F	% V	% F	% V	% F	% V	% F	% V
Unidentified matter		57.14	42.20	35.00	7.01	23.33	5.50	31.71	7.35
Sand grains		4.76	4.76	1.67	0.08	0.00	0.00	0.00	0.00
Fish egg		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Algae		47.62	35.32	8.33	1.23	0.00	0.00	0.00	0.00
Terrestrial invertebrates		0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.12
Fish larvae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrate egg		0.00	0.00	23.33	2.89	13.33	2.75	9.76	0.63
Plant material		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Testate		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera		4.76	2.38	3.33	0.00	0.00	0.00	0.00	0.00
Cladocera	Chydoridae	14.29	10.58	78.33	27.55	50.00	16.72	68.29	11.95
	Ilyocryptidae	0.00	0.00	0.00	0.00	3.33	0.15	17.07	1.35
	Macrothricidae	0.00	0.00	23.33	3.11	33.33	3.00	48.78	11.39
	Sididae	4.76	4.76	1.67	0.60	6.67	3.87	7.32	0.68
	Daphniidae	0.00	0.00	28.33	7.90	10.00	0.90	7.32	0.71
	Bosminidae	0.00	0.00	1.67	0.14	0.00	0.00	2.44	0.00
	Moinidae	0.00	0.00	1.67	0.15	0.00	0.00	0.00	0.00
Copepoda	Copepod naupli	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyclopoida	0.00	0.00	75.00	26.93	66.67	18.17	58.54	5.41
	Calanoida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Harpacticoida	0.00	0.00	11.67	1.25	10.00	0.15	19.51	0.50
Tardigrada		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda		0.00	0.00	0.00	0.00	6.67	0.61	0.00	0.00
Ostracoda		0.00	0.00	11.67	1.36	23.33	2.89	36.59	5.96
Decapoda	Shrimp larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca		0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.54
Nematoda		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oligochaeta		0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.27
Arachnida	Hydrachnidae	0.00	0.00	6.67	0.68	0.00	0.00	7.32	0.26
Collembola		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera		0.00	0.00	3.33	1.14	0.00	0.00	7.32	0.91
Ephemeroptera		0.00	0.00	0.00	0.00	6.67	0.89	4.88	0.65
Diptera	Chironomidae larvae	0.00	0.00	48.33	16.41	76.67	39.32	73.17	22.46
	Chironomidae pupae	0.00	0.00	0.00	0.00	6.67	2.85	9.76	1.42
	Simulidae	0.00	0.00	1.67	0.63	0.00	0.00	0.00	0.00
	Simulidae pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Unid. diptera larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Unid. diptera pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Culicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Tipulidae	0.00	0.00	0.00	0.00	3.33	1.67	4.88	2.48
Hemiptera	Corixidae	0.00	0.00	1.67	0.35	3.33	0.56	63.41	24.16
	Mesoveliidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gerridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neuroptera		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Carp diet cont.

Developmental stage		PR		PF		M		JA	
No. Fish		21		60		30		41	
		% F	% V	% F	% V	% F	% V	% F	% V
Coleoptera larvae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera adult		0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.81
Megaloptera	Sialidae	0.00	0.00	1.67	0.61	0.00	0.00	0.00	0.00

(b) Australian smelt

Developmental stage		PR		PF		M		JA	
No. Fish		73		28		60		123	
		% F	% V	% F	% V	% F	% V	% F	% V
Unidentified matter		43.84	32.53	28.57	13.45	60.00	20.01	25.20	6.82
Sand grains		12.33	8.61	3.57	0.60	0.00	0.00	0.81	0.07
Fish egg		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Algae		4.11	5.71	17.86	4.17	15.00	1.49	0.00	0.00
Terrestrial invertebrates		0.00	0.00	0.00	0.00	31.67	12.36	40.65	13.22
Fish larvae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrate egg		0.00	0.00	0.00	0.00	3.33	0.14	1.63	0.22
Plant material		0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.10
Testate		0.00	0.00	3.57	0.89	3.33	0.21	1.63	0.00
Rotifera		49.32	37.49	64.29	35.32	21.67	8.34	0.00	0.00
Cladocera	Chydoridae	0.00	0.00	25.00	8.16	43.33	9.06	10.57	1.41
	Ilyocryptidae	0.00	0.00	3.57	0.71	6.67	0.70	4.88	0.32
	Macrothricidae	1.37	0.91	28.57	11.17	33.33	7.59	4.88	0.50
	Sididae	0.00	0.00	3.57	1.07	6.67	1.38	0.00	0.00
	Daphniidae	0.00	0.00	7.14	0.92	18.33	2.06	4.07	0.83
	Bosminidae	0.00	0.00	10.71	1.99	6.67	0.78	0.00	0.00
	Moinidae	0.00	0.00	3.57	1.79	3.33	0.56	0.00	0.00
Copepoda	Copepod nauplii	19.18	12.47	28.57	10.54	15.00	2.51	0.00	0.00
	Cyclopoida	4.11	2.28	21.43	8.11	23.33	7.72	3.25	0.48
	Calanoida	0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.33
	Harpacticoida	0.00	0.00	0.00	0.00	16.67	3.18	5.69	0.75
Tardigrada		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda		0.00	0.00	0.00	0.00	6.67	0.56	3.25	0.36
Decapoda	Shrimp larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.18
Mollusca		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nematoda		0.00	0.00	0.00	0.00	10.00	1.89	9.76	1.88
Oligochaeta		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arachnida	Hydrachnidae	0.00	0.00	0.00	0.00	16.67	2.28	13.82	0.56
Collembola		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera		0.00	0.00	0.00	0.00	3.33	0.49	5.69	1.06
Ephemeroptera		0.00	0.00	0.00	0.00	6.67	1.10	11.38	2.90
Diptera	Chironomidae larvae	0.00	0.00	10.71	1.10	50.00	10.21	65.04	11.79
	Chironomidae pupae	0.00	0.00	0.00	0.00	10.00	3.97	86.18	52.34
	Simulidae larvae	0.00	0.00	0.00	0.00	1.67	0.30	0.81	0.20
	Simulidae pupae	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.35
	Unid. Diptera larvae	0.00	0.00	0.00	0.00	0.00	0.00	1.63	0.30
	Unid. Diptera pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Culicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Australian smelt diet cont.

	Developmental stage	PR		PF		M		JA	
	No. Fish	73		28		60		123	
		% F	% V	% F	% V	% F	% V	% F	% V
Hemiptera	Corixidae	0.00	0.00	0.00	0.00	1.67	0.14	6.50	1.08
	Mesoveliidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gerridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neuroptera		0.00	0.00	0.00	0.00	5.00	0.97	0.00	0.00
Coleoptera larvae		0.00	0.00	0.00	0.00	0.00	0.00	1.63	0.23
Coleoptera adult		0.00	0.00	0.00	0.00	0.00	0.00	4.88	1.73
Megaloptera	Sialidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(c) Gambusia

	Developmental stage	PL1		PL2		JA	
	No. Fish	54		127		201	
		% F	% V	% F	% V	% F	% V
Unidentified matter		64.81	24.99	43.31	9.79	32.84	8.79
Sand grains		3.70	1.08	0.00	0.00	0.50	0.04
Fish egg		0.00	0.00	0.00	0.00	0.00	0.00
Algae		7.41	0.36	12.60	0.35	0.50	0.00
Terrestrial invertebrates		5.56	1.76	22.05	4.88	43.28	13.73
Fish larvae		0.00	0.00	0.00	0.00	0.00	0.00
Invertebrate egg		11.11	1.77	5.51	0.57	2.49	0.21
Plant material		0.00	0.00	0.00	0.00	0.00	0.00
Testate		0.00	0.00	1.57	0.05	1.49	0.05
Rotifera		37.04	8.61	23.62	4.36	0.50	0.00
Cladocera	Chydoridae	46.30	10.05	62.99	14.13	36.32	5.36
	Ilyocryptidae	5.56	0.46	5.51	0.45	2.49	0.16
	Macrothricidae	29.63	8.15	55.12	8.78	34.33	3.43
	Sididae	5.56	1.79	5.51	0.74	6.97	0.78
	Daphniidae	16.67	5.16	18.90	2.62	16.92	3.43
	Bosminidae	0.00	0.00	0.00	0.00	1.00	0.08
	Moinidae	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	Copepod nauplii	1.85	0.19	2.36	0.07	0.00	0.00
	Cyclopoida	68.52	28.49	77.95	28.49	39.80	7.13
	Calanoida	0.00	0.00	0.00	0.00	0.00	0.00
	Harpacticoida	5.56	1.34	6.30	0.50	4.48	0.31
Tardigrada		1.85	0.66	1.57	0.11	0.00	0.00
Isopoda		0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda		1.85	0.09	3.15	0.38	2.49	0.24
Decapoda	Shrimp larvae	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca		0.00	0.00	0.00	0.00	1.49	0.23
Nematoda		1.85	0.40	0.00	0.00	1.99	0.42
Oligochaeta		0.00	0.00	0.00	0.00	0.00	0.00
Arachnida	Hydrachnidae	3.70	0.28	6.30	0.36	7.96	0.31
Collembola		0.00	0.00	9.45	1.52	7.96	1.15
Trichoptera		1.85	0.93	2.36	0.47	6.97	0.96
Ephemeroptera		1.85	0.46	1.57	0.31	10.95	3.42

Gambusia diet cont.

	Developmental stage	PL1		PL2		JA	
	No. Fish	54		127		201	
		% F	% V	% F	% V	% F	% V
Diptera	Chironomidae larvae	14.81	2.23	34.65	7.62	40.30	9.59
	Chironomidae pupae	0.00	0.00	18.11	7.38	54.73	20.53
	Simulidae larvae	0.00	0.00	0.00	0.00	1.99	0.30
	Simulidae pupae	0.00	0.00	0.00	0.00	1.00	0.40
	Unid. diptera larvae	0.00	0.00	0.79	0.33	2.49	0.90
	Unid. diptera pupae	0.00	0.00	3.94	1.29	1.49	0.66
	Culicidae	0.00	0.00	0.79	0.62	0.00	0.00
	Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00
Hemiptera	Corixidae	0.00	0.00	14.17	3.25	39.80	14.67
	Mesoveliidae	0.00	0.00	0.00	0.00	0.50	0.12
	Gerridae	0.00	0.00	0.79	0.14	11.94	2.41
Neuroptera		0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera larvae		0.00	0.00	2.36	0.43	0.00	0.00
Coleoptera adult		3.70	0.74	0.00	0.00	1.49	0.18
Megaloptera	Sialidae	0.00	0.00	0.00	0.00	0.00	0.00

(d) Rainbowfish

	Developmental stage	PR		PF		M		JA	
	No. Fish	83		95		127		142	
		% F	% V	% F	% V	% F	% V	% F	% V
Unidentified matter		83.13	37.89	87.37	34.05	77.95	18.98	42.96	8.85
Sand grains		1.20	0.45	0.00	0.00	0.00	0.00	0.00	0.00
Fish egg		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Algae		59.04	32.01	46.32	14.67	37.80	6.68	13.38	1.94
Terrestrial invertebrate		0.00	0.00	3.16	0.57	25.98	5.79	89.44	32.50
Fish larvae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrate egg		0.00	0.00	0.00	0.00	1.57	0.11	7.04	0.85
Plant material		0.00	0.00	0.00	0.00	0.79	0.07	2.82	0.45
Testate		3.61	0.14	5.26	0.09	14.17	0.32	7.75	0.56
Rotifera		80.72	24.17	86.32	21.73	62.99	8.32	9.86	1.79
Cladocera	Chydoridae	2.41	0.55	14.74	2.15	29.92	5.21	18.31	1.37
	Ilyocryptidae	1.20	0.40	15.79	4.73	28.35	6.75	11.27	0.53
	Macrothricidae	4.82	1.23	38.95	9.84	63.78	19.48	40.14	3.00
	Sididae	0.00	0.00	1.05	0.18	8.66	1.33	4.93	0.13
	Daphniidae	0.00	0.00	4.21	0.71	19.69	2.41	9.86	0.45
	Bosminidae	0.00	0.00	0.00	0.00	1.57	0.14	0.70	0.00
	Moinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	Copepod nauplii	9.64	1.88	6.32	0.51	15.75	1.06	1.41	0.04
	Cyclopoida	2.41	0.22	12.63	2.18	26.77	3.54	17.61	1.25
	Calanoida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Harpacticoida	1.20	0.27	15.79	3.09	27.56	3.34	17.61	0.65
Tardigrada		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda		2.41	0.18	4.21	0.25	30.71	2.17	18.31	0.74
Decapoda	Shrimp larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca		0.00	0.00	0.00	0.00	1.57	0.17	3.52	0.43
Nematoda		0.00	0.00	2.11	0.11	3.15	0.29	3.52	0.27
Oligochaeta		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Rainbowfish diet cont.

	Developmental stage	PR		PF		M		JA	
	No. Fish	83		95		127		142	
		% F	% V	% F	% V	% F	% V	% F	% V
Arachnida	Hydrachnidae	1.20	0.10	2.11	0.11	17.32	2.54	14.08	0.72
Collembola		0.00	0.00	7.37	2.17	23.62	3.66	24.65	2.93
Trichoptera		0.00	0.00	2.11	0.39	12.60	1.35	14.79	0.88
Ephemeroptera		0.00	0.00	0.00	0.00	2.36	0.55	12.68	1.91
Diptera	Chironomidae larvae	2.41	0.51	16.84	2.49	29.92	3.71	40.85	4.75
	Chironomidae pupae	0.00	0.00	0.00	0.00	6.30	1.43	66.20	13.83
	Simulidae larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Simulidae pupae	0.00	0.00	0.00	0.00	0.79	0.11	15.49	1.80
	Unid. diptera larvae	0.00	0.00	0.00	0.00	0.79	0.14	0.70	0.03
	Unid. diptera pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Culicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemiptera	Corixidae	0.00	0.00	0.00	0.00	2.36	0.39	48.59	13.32
	Mesoveliidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gerridae	0.00	0.00	0.00	0.00	0.00	0.00	14.08	1.22
Neuroptera		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera larvae		0.00	0.00	0.00	0.00	0.00	0.00	2.11	0.18
Coleoptera adult		0.00	0.00	0.00	0.00	0.00	0.00	17.61	2.65
Megaloptera	Sialidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(e) Carp gudgeons

	Developmental stage	PR		PF		M		JA	
	No. Fish	8		5		4		59	
		% F	% V	% F	% V	% F	% V	% F	% V
Unidentified matter		25.00	5.42	20.00	2.00	50.00	4.36	27.12	9.08
Sand grains		0.00	0.00	0.00	0.00	0.00	0.00	8.47	1.06
Fish egg		0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.65
Algae		0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.27
Terrestrial invertebrate		0.00	0.00	0.00	0.00	0.00	0.00	11.86	3.08
Fish larvae		0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.34
Invertebrate egg		0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.08
Plant material		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Testate		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera		0.00	0.00	0.00	0.00	100.00	18.53	11.86	1.50
Cladocera	Chydoridae	0.00	0.00	0.00	0.00	0.00	0.00	54.24	9.40
	Ilyocryptidae	0.00	0.00	0.00	0.00	0.00	0.00	18.64	1.22
	Macrothricidae	0.00	0.00	0.00	0.00	0.00	0.00	23.73	1.74
	Sididae	0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.08
	Daphniidae	0.00	0.00	0.00	0.00	0.00	0.00	11.86	2.39
	Bosminidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Moinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	Copepod nauplii	100.00	94.58	100.00	98.00	100.00	51.62	18.64	3.67
	Cyclopoida	0.00	0.00	0.00	0.00	100.00	25.49	74.58	19.80
	Calanoida	0.00	0.00	0.00	0.00	0.00	0.00	3.39	1.08
	Harpacticoida	0.00	0.00	0.00	0.00	0.00	0.00	13.56	1.32
Tardigrada		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda		0.00	0.00	0.00	0.00	0.00	0.00	20.34	1.82

Carp gudgeon diet cont.

	Developmental stage	PR		PF		M		JA	
	No. Fish	8		5		4		59	
		% F	% V	% F	% V	% F	% V	% F	% V
Decapoda	Shrimp larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca		0.00	0.00	0.00	0.00	0.00	0.00	3.39	0.49
Nematoda		0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.19
Oligochaeta		0.00	0.00	0.00	0.00	0.00	0.00	6.78	0.44
Arachnida	Hydrachnidae	0.00	0.00	0.00	0.00	0.00	0.00	5.08	0.26
Collembola		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera		0.00	0.00	0.00	0.00	0.00	0.00	5.08	0.59
Ephemeroptera		0.00	0.00	0.00	0.00	0.00	0.00	15.25	3.14
Diptera	Chironomidae larvae	0.00	0.00	0.00	0.00	0.00	0.00	81.36	27.73
	Chironomidae pupae	0.00	0.00	0.00	0.00	0.00	0.00	8.47	0.97
	Simulidae larvae	0.00	0.00	0.00	0.00	0.00	0.00	6.78	1.25
	Simulidae pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Unid. diptera larvae	0.00	0.00	0.00	0.00	0.00	0.00	3.39	0.19
	Unid. diptera pupae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Culicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemiptera	Corixidae	0.00	0.00	0.00	0.00	0.00	0.00	30.51	6.20
	Mesoveliidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gerridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neuroptera		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera larvae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera adult		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Megaloptera	Sialidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(f) Murray cod

	Developmental stage	PL.	
	No. Fish	73	
		% F	% V
Unidentified matter		27.40	15.00
Sand grains		9.59	6.39
Fish egg		0.00	0.00
Algae		0.00	0.00
Terrestrial invertebrate		0.00	0.00
Fish larvae		0.00	0.00
Invertebrate egg		0.00	0.00
Plant material		0.00	0.00
Testate		0.00	0.00
Rotifera		0.00	0.00
Cladocera	Chydoridae	16.44	8.45
	Ilyocryptidae	5.48	2.49
	Macrothricidae	46.58	29.66
	Sididae	0.00	0.00
	Daphniidae	1.37	1.20
	Bosminidae	0.00	0.00
	Moinidae	0.00	0.00

Murray cod cont.

	Developmental stage	PL	
	No. Fish	73	
		% F	% V
Copepoda	Copepod nauplii	0.00	0.00
	Cyclopoida	35.62	17.31
	Calanoida	0.00	0.00
	Harpacticoida	0.00	0.00
Tardigrada		0.00	0.00
Isopoda		0.00	0.00
Ostracoda		1.37	0.46
Decapoda	Shrimp larvae	0.00	0.00
Mollusca		0.00	0.00
Nematoda		0.00	0.00
Oligochaeta		0.00	0.00
Arachnida	Hydrachnidae	0.00	0.00
Collembola		0.00	0.00
Trichoptera		0.00	0.00
Ephemeroptera		2.74	2.28
Diptera	Chironomidae larvae	20.55	8.63
	Chironomidae pupae	9.59	6.46
	Simulidae larvae	2.74	1.68
	Simulidae pupae	0.00	0.00
	Unid. diptera larvae	0.00	0.00
	Unid. diptera pupae	0.00	0.00
	Culicidae	0.00	0.00
	Tipulidae	0.00	0.00
Hemiptera	Corixidae	0.00	0.00
	Mesoveliidae	0.00	0.00
	Gerridae	0.00	0.00
Neuroptera		0.00	0.00
Coleoptera larvae		0.00	0.00
Coleoptera adult		0.00	0.00
Megaloptera	Sialidae	0.00	0.00

Appendix C: List of Potential Larval Fish Prey Items and Categorisation into Habitat Zones.

Prey item		Habitat zone
Unid matter		Other
Sand grains		Other
Fish egg		Other
Algae		Both epibenthic & pelagic
Terrestrial invertebrate		Surface
Fish larvae		Other
Invertebrate egg		Epibenthic
Plant material		Other
Testate		Epibenthic
Rotifera		Pelagic
Cladocera	Chydoridae	Epibenthic
	Ilyocryptidae	Epibenthic
	Macrothricidae	Epibenthic
	Sididae	Pelagic
	Daphniidae	Pelagic
	Bosminidae	Pelagic
	Moinidae	Pelagic
Copepoda	Copepod nauplii	Pelagic
	Cyclopoida	Pelagic
	Calanoid	Pelagic
	Harpacticoid	Epibenthic
Tardigrada		Epibenthic
Isopoda		Epibenthic
Ostracoda		Epibenthic
Decapoda	Shrimp larvae	Epibenthic
Mollusc		Epibenthic
Nematoda		Other
Oligochaeta		Epibenthic
Arachnida	Hydrachnidae	Epibenthic
Collembola		Surface
Trichoptera		Epibenthic
Ephemeroptera		Epibenthic
Diptera	Chironomid	Epibenthic
	Chironomid pupae	Both epibenthic & pelagic
	Simulid	Epibenthic
	Simulidae pupae	Epibenthic
	Unid diptera larvae	Epibenthic
	Culicidae	Surface
	Unid diptera pupae	Both epibenthic & pelagic
	Tipulidae	Epibenthic
Hemiptera	Corixidae	Both epibenthic & pelagic
	Mesoveliidae	Surface
	Gerridae	Surface
Neuroptera		Epibenthic
Coleoptera	Coleoptera larvae	Epibenthic
	Coleoptera adult	Epibenthic
Megaloptera	Sialidae	Epibenthic

Appendix D: Pilot Study for Sampling Larval and Juvenile Fish on the Ovens River Flood plain

Aims

The aim of the pilot study was to conduct preliminary sampling on the floodplain environment during flood events. Specifically, to:

- determine the feasibility of sampling on the floodplain
- determine the variability among sites
- determine the sampling success of some of the commonly used fish larvae sampling methods

Methods

Sampling sites and trips

Sampling was conducted at three sites on the Ovens River downstream of Wangaratta. Peechalba (146° 14' 30'', 36° 9' 60'') and Killawarra sites are in two State Forest reserves, while Duffus road site was on private property. Sampling was conducted during periods of floodplain inundation on 8 October and 17 November 1998, and during within channel flows on 24 October (Figure 2.9a).

Sampling gear and design

A range of gear types was used for the pilot study, including light traps, sweep net, drift and hand trawl. The SNE method was not trialed during this study. Modified quadrefoil light traps have been used to sample fish larvae in riverine environment in recent years (Humphries and Lake 2000, Humphries *et al.* in press). For a full description of the method see Humphries *et al.* (in press). A standard 250 µm mesh sweep net (30 cm x 30 cm) was used to sample fish larvae in wadable depths on the floodplain environment. The mesh net tapered into a removable sample collection jar. One sweep net sample consisted of a timed 30 second sweep, moving in a forward, and up and down sweeping motion, to sample all depths available and to limit herding small fish. Since the sweep net was limited to wadeable depths, hand trawl sampling was conducted in deeper habitats. For a full description of the hand trawl and drift nets see section 3.2. Sweep and hand trawl net samples were conducted during the day, light traps were set overnight, and drift nets were set for three hours both during the day and night. Sampling was conducted randomly

throughout the available habitat types on the floodplain for most methods, except for the drift, which was only collected in anabranch habitats.

Due to the availability of equipment, the number of samples taken for some methods was not consistent across sampling dates (Table D.1). A total of 15 hand trawl and sweep net samples and at least five light traps samples, were taken randomly at the two sites on each sampling trip. At least one (mostly two) drift net samples were collected from the anabranch during the day and night.

Table D.1: The number of samples taken with all methods during the study. (D) = day, (N) = night.

Date	Site	Light trap	Sweep net	Hand trawl	Drift net
8 October	Peechalba	10	10	10	2 (D) 2 (N)
	Duffus Rd	5	5	5	0
24 October	Peechalba	5	10	10	1 (D) 1 (N)
	Killawarra	0	5	5	0
17 November	Peechalba	5	10	10	2 (D) 2 (N)
	Killawarra	0	5	5	-0
	Total no. samples	**25**	**45**	**45**	**10**

Microhabitat variables

At least three randomly selected points were used to sample water quality variables at each site at every sampling time. Temperature, dissolved oxygen, turbidity and pH were measured using a Horiba™ U10 water quality checker. A number of microhabitat variables were measured at each sweep net, light trap and hand trawl sampling location. These were similar variables as were measured in the true floodplain sampling (Chapter 6), but are not discussed further in the pilot study.

Preservation and laboratory methods

All samples were preserved in 95 % ethanol, and returned to the laboratory where the fish were removed from the samples using a dissecting microscope. Identifications were made using published and unpublished descriptions and keys (Lake 1967b, McDowall, 1996; Neira *et al.* 1998; Humphries, unpub. data., see Appendix A). For the purposes of the pilot

study only, fish were categorised as either larvae or juveniles/adults. Individual fish were classified as juvenile/adults when all rays in all fins were fully developed.

Data analysis

Site comparisons were only made between Peechalba and Killawarra, for the second and third sampling trip only, comparing hand trawl and sweep net catches. Results were standardised for ten hand trawl and ten sweep net samples at each site and trip. A comparison of methods was only made at Peechalba, since this site was sampled on all three sampling occasions. Results were again standardised across each trip, at ten sweep net, ten hand trawl, ten light trap and two day and two night drift net samples.

Results and discussion

Practical considerations

Duffus road was an unsuitable site to sample on the last two sampling trips, since floodplain inundation only occurred during the first and much higher flood (Figure 2.9a). The site at Killawarra could not be sampled during the first sampling trip, since the height of the flood restricted walking access to the floodplain. In general, the site at the Peechalba bridge had much easier access to the floodplain during different water level heights. The elevated sealed road across the full width of the floodplain, allowed easy access to a range of habitat types, including billabongs, anabranch and floodplain habitats.

All sampling methods were possible during the different water level heights, however light traps were a problem during the receding arm of the flood, as the falling water levels could leave the traps dry. From previous studies using light traps, sampling in billabongs environments can be problematic due to low dissolved oxygen rates at night will kill larvae, making identification difficult (King, pers. obs.). It was also noted that drift sampling within the main channel environment was possible, and may prove useful to establish species present within the main channel environment during flood periods (especially main channel species such as Murray cod and golden perch)

Comparison of sites

A higher number of fish were collected at Killawarra than at Peechalba, using both the hand trawl and sweep net methods (Table D.2). Larvae and juveniles/adults of Australian

smelt and carp gudgeon larvae were captured in higher numbers at both Killawarra than Peechalba. However all stages of all four species were found at Peechalba using both the hand trawl and sweep net methods.

Table D.2: Average number of fish captured in hand trawl and sweep net samples at Killawarra (KI) and Peechalba (PE) sites, across trip 1 and 2.

		Hand trawl		Sweep net	
Species	Stage	KI	PE	KI	PE
Carp	Larvae	0.0	24.0	6.0	23.5
	Juveniles	0.0	0.0	0.0	4.0
Australian smelt	Larvae	105.0	52.5	14.0	10.5
	Juveniles/Adults	41.0	12.5	0.0	0.5
Redfin perch	Larvae	0.0	0.5	0.0	0.0
	Juveniles	0.0	0.0	0.0	0.0
Carp gudgeons	Larvae	44.0	13.0	342.0	1.5
	Juveniles/Adults	0.0	1.0	3.0	0.5
	Total no. larvae	**149.0**	**90.0**	**362.0**	**35.5**
	Total no. Juveniles/Adults	**41.0**	**3.0**	**13.5**	**5.0**
	Total no. fish	**190.0**	**103.5**	**365.0**	**40.5**

Comparison of methods

Drift net samples collected the greatest number of fish per sample of the four methods used (Table D.3). Drift net catches were dominated by carp larvae and were very poor in catches of juveniles/adults of all species. Light trap samples collected the greatest number of juveniles/adults per sample, but also caught the lowest number of larvae per sample. Light traps captured all stages of all species, except redfin larvae. Hand trawl and sweep nets caught most stages of the species, but in lower number per sample than either light traps or drift nets.

Table D.3: Average number of fish captured in drift nets, hand trawls, light traps and sweep net samples at Peechalba (PE) sites across the three sampling trips.

Species	Stage	Drift	Hand trawl	Light trap	Sweep net
Carp	Larvae	71.67	16.00	2.33	50.00
	Juveniles	0.33	0.00	11.33	2.67
Australian smelt	Larvae	1.33	35.00	8.67	7.00
	Juveniles/Adults	0.67	8.33	42.33	0.33
Redfin	Larvae	0.00	0.33	0.00	0.00
	Juveniles	0.00	0.00	7.33	0.00
Carp gudgeons	Larvae	7.33	8.67	5.33	1.00
	Juveniles/Adults	0.67	0.67	29.00	0.67
	Total no. larvae	80.33	60.00	16.33	58.00
	Total no. Juveniles/Adults	16.70	9.00	90.00	3.67
	Total no. fish	82.00	69.00	106.33	61.67
	No. samples	12	30	30	30
	Avg. no. larvae/sample	6.69	2.00	0.54	1.93
	Avg. no. JA per sample	0.14	0.30	3.00	0.12
	Avg. no. fish per sample	6.83	2.30	3.54	2.06

Conclusions

Although sampling was conducted to determine the best methods and sites as well as the feasibility of the study, practical considerations were the main lessons learnt from this pilot study. Peechalba was chosen as the site for future work, since access to the river and floodplain habitats at various water levels could not be guaranteed at either Killawarra or Duffus road.

Light traps captured a greater number of fish per sample compared to the other methods, however, the method was not used in future work as it is not habitat specific and problems were encountered with falling water levels and night time low dissolved oxygen levels. Sweep net sampling was also not used in future work, but was replaced with the newly developed SNE method (see Chapter 2). Drift net and hand trawl sampling was retained for future work. Drift net sampling could also be conducted in the main channel environment.

References

Ahlstrom E. H., Butler J. L. and Sumida B. Y. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. *Bulletin of Marine Sciences* **26**, 285-402.

Allen G. R. 1989. *Freshwater Fishes of Australia*. T.F.H. publications, Neptune City, New Jersey, USA.

Appleford P., Anderson T. A. and Gooley G. J. 1998. Reproductive cycle and gonadal development of Macquarie perch, *Macquaria australasica* Cuvier (Percichthyidae), in Lake Dartmouth and tributaries of the Murray-Darling Basin, Victoria, Australia. *Marine and Freshwater Research* **49**, 163-9.

Armstrong M. L. and Brown A. V. 1983. Diel drift and feeding of channel catfish alevines in the Illinois River, Arkansas. *Transactions of the American Fisheries Society* **112**, 302-7.

Arthington A. H. 1989. Diet of *Gambusia affinis holbrooki, Xiphophorus helleri, X. maculatus* and *Poecilia reticulata* (Pisces: Poeciliidae) in streams of southeastern Queensland, Australia. *Asian Fisheries Science* **2**, 193-212.

Arthington A. H., Milton D. A. and McKay R. J. 1983. Effects of urban development and habitat alteration on the distribution and abundance of native and exotic freshwater fish in the Brisbane region, Queensland. *Australian Journal of Ecology* **8**, 87-101.

Arthington A. H. and Lloyd L. N. 1989. Chapter 18: Introduced Poeciliids in Australia and New Zealand. *In.* Meffe G. K. and Snelson F. F. (Eds.). *Ecology and Evolution of livebearing fishes (*Poeciliidae*)*. Prentice-Hall. New Jersey, USA. pp 333-47.

Arumugam P. T. and Geddes M. C. 1987. Feeding and growth of golden perch larvae and fry (*Macquaria ambigua* Richardson). *Transactions of the Royal Society of South Australia* **111**, 59-65.

ASFB. 2001. Conservation status of Australian fishes – 2001. *Australian Society for Fish Biology Newsletter* **31**, 37-41.

Backhouse G. N. and Frusher D. J. 1980. The crimson-spotted rainbowfish, *Melanotaenia fluviatilis* (Castelnau 1878). *Victorian Naturalist* **97**, 144-8.

Balon E. K. 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of Fisheries Research Board of Canada* **32**, 821-64.

Balon E. K. 1981. Additions and amendments to the classification of reproductive styles in fishes. *Environmental Biology of Fishes* **6**, 377-89.

Balon E. K. 1984. Reflections on some decisive events in the early life of fishes. *Transactions of the American Fisheries Society* **113**, 178-85.

Balon E. K. 1986. Types of feeding in the ontogeny of fishes and the life-history model. *Environmental Biology of Fishes* **16**, 11-24.

Baras E. and Nindaba J. 1999a. Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. *Environmental Biology of Fishes* **53**, 183-97.

Baras E. and Nindaba J. 1999b. Diel dynamics of habitat use by riverine young-of-the-year *Barbus barbus* and *Chondrostoma nasus* (Cyprinidae). *Archiv für Hydrobiologie* **146**, 431-48.

Bass J. A. B., Pinder L. C. V. and Leach D. V. 1997. Temporal and spatial variation in zooplankton populations in the River Great Ouse: an ephemeral food resource for larval and juvenile fish. *Regulated Rivers: Research and Management* **13**, 245-58.

Basu B. K. and Pick F. R. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnology and Oceanography* **41**, 1572-7.

Bayley P. B. 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers: Research and Management* **6**, 75-86.

Bayley P. B. 1995. Understanding large river-floodplain ecosystems. *BioScience* **45**, 153-8.

Begon M., Harper J. L. and Townsend C. R. 1990. *Ecology. Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, USA.

Benke A. C., Chaubey I., Ward G. M. and Dunn E. L. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. *Ecology* **81**, 2730-41.

Bertozzi T., Adams M. and Walker K.F. 2000. Species boundaries in carp gudgeons (Eleotrididae: *Hypseleotris*) from the River Murray, South Australia: evidence for multiple species and extensive hybridization. *Marine and Freshwater Research* **51**, 805-15.

Blaxter J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* **115**, 98-114.

Boehlert G. W. and Mundy B. C. 1988. Roles of behavioural and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**, 51-67.

Bone Q., Marshall N. B. and Blaxter J. H. S. 1995. *Biology of Fishes*. 2nd edition. Blackie Academic and Professional Publishers, Glasgow, UK.

Bonetto A. A., Dioni W. and Pignalberi C. 1969. Limnological investigations on biotic communities in the middle Parana River valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **17**, 1035-1050.

Boulton A. J. and Brock M. A. 1999. *Australian Freshwater Ecology. Processes and Management*. Gleaneagles Publishing, Glen Osmond, Australia.

Boulton A. J. and Lloyd L. N. 1992. Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia. *Regulated Rivers: Research and Management* **7**, 137-51.

Bowen S. H. 1996. Chapter 17: Quantitative description of the diet. *In.* Murphy, B. R., and Willis D. W. (Ed.). *Fisheries Techniques*. American Fisheries Society. Bethesda, USA. pp 513-32.

Brander K. M., Dickson R. R. and Shepherd J. G. 2001. Modeling the timing of plankton production and its effect on recruitment of cod (*Gadus morhua*). *ICES Journal of*

Marine Science **58**, 962-6.

Bremigan M. T. and Stein R. A. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 913-22.

Brewer R. 1988. *The Science of Ecology*. Saunders College Publishing, Florida, USA.

Brittain J. E. and Eikeland T. J 1988. Invertebrate drift - a review. *Hydrobiologia* **166**, 77-93.

Brooks J. J. 1997. *Trophic Ecology of a Freshwater Crayfish, Cherax destructor Clark, in Billabongs of South-Eastern Australia*. Department of Ecology and Evolutionary Biology, Monash University, Victoria, Australia. PhD thesis.

Brosse S., Gabas S., Cever K. and Lak S. 1999. Comparison of two point abundance sampling methods to assess young roach (*Rutilus rutilus* L.) microhabitat in the littoral zone of Lake Pareloup (France). *Annales de Limnologie* **35**, 199-204.

Brown A. V. and Armstrong M. L. 1985. Propensity to drift downstream among various species of fish. *Journal of Freshwater Ecology* **3**, 3-17.

Bult T. P., Haedrich R. L. and Schneider D. C. 1998. New technique describing spatial scaling and habitat selection in riverine habitats. *Regulated Rivers: Research and Management* **14**, 107-18.

Byström P., Persson L. and Wahlström E. 1998. Competing predators and prey: juvenile bottlenecks in whole-lake experiments. *Ecology* **79**, 2153-67.

Cadwallader P. L. 1977. *J.O. Langtry's 1949-50 Murray River Investigations*. Ministry for Conservation Fisheries and Wildlife Division, Victoria, Australia.

Cadwallader P. L. 1978. Some causes of the decline in range and abundance of native fish in the Murray-Darling river system. *Proceedings of the Royal Society of Victoria* **90**, 211-24.

Cadwallader P. L. and Lawrence B. 1990. Chapter 22: Fish. *In.* Mackay N. and Eastburn D. (Eds.). *The Murray*. Murray Darling Basin Commission. Canberra, Australia. pp

317-63.

Cadwallader P. L. and Rogan P. L. 1977. The Macquarie perch, *Macquaria australasica* (Pisces: Percichthyidae) of Lake Eildon, Victoria. *Australian Journal of Ecology* **2**, 409-18.

Cadwallader P. L., Eden A. K. and Hook R. A. 1980. Role of streamside vegetation as a food source for *Galaxias olidus* Günther (Pisces: Galaxiidae). *Australian Journal of Marine and Freshwater Research* **31**, 257-62.

Cederholm C. J., Bilby R. E., Bisson P. A., Bumstead T. W., Fransen B. R., Scarlett W. J. and Ward J. W. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. *North American Journal of Fisheries Management* **17**, 947-63.

Close A. 1990. The impact of man on the natural flow regime. *In.* Mackay N. and Eastburn D. (Eds.). *The Murray.* Murray-Darling Basin Commission. Canberra, Australia. pp 61-76.

Copp G. H. 1989a. Electrofishing for fish larvae and 0+ juveniles: equipment modifications for increased efficiency with short fishes. *Aquaculture and Fisheries Management* **20**, 453-62.

Copp G. H. 1989b. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* **26**, 1-27.

Copp G. H. 1990. Shifts in the microhabitat of larval and juvenile roach, *Rutilis rutilus* (L.), in a floodplain channel. *Journal of Fish Biology* **36**, 683-92.

Copp G. H. 1992a. An empirical model for predicting microhabitat of 0+ juvenile fishes in a lowland river catchment. *Oecologia* **91**, 338-45.

Copp G. H. 1992b. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. *Environmental Biology of Fishes* **33**, 181-93.

Copp G. H. 1993. The upper Rhone River revisited: an empirical model of microhabitat use by 0+ juvenile fishes. *Folia Zoologica* **42**, 329-40.

Copp G. H. and Penaz M. 1988. Ecology of fish spawning and nursery zones in the floodplain, using a new sampling approach. *Hydrobiologia* **169**, 209-24.

Copp G. H. and Jurajda P. 1993. Do small riverine fish move inshore at night? *Journal of Fish Biology* **43**, 229-41.

Copp G. H., Guti G., Rovny B. and Cerny J. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak floodplain of the Danube River. *Environmental Biology of Fishes* **40**, 329-348.

Copp G. H. and Garner P. 1995. Evaluating the microhabitat use of freshwater fish larvae and juveniles with point abundance sampling by electrofishing. *Folia Zoologica* **44**, 145-58.

Cottingham P., Hannon G., Hillman T., Humphries P., Metzeling L., Roberts J. and Stewardson M. 2001a. *Draft only: Report of the Broken Scientific Panel on the Environmental Condition and Flows of the Broken River and Broken Creek.* Cooperative Research Centre for Freshwater Ecology, Department of Natural Resources and Environment, Victoria, Australia.

Cottingham P., Hannon G., Hillman T., Koehn J., Metzeling L., Roberts J. and Rutherfurd I. 2001b. *Draft only: Report of the Ovens Scientific Panel on the Environmental Condition and Flow in the Ovens River.* Cooperative Research Centre for Freshwater Research, Department of Natural Resources and Environment, Victoria, Australia.

Crabb P. 1997. *Murray-Darling Basin Resources.* Murray-Darling Basin Commission. Canberra, Australia.

Crome F. H. J. 1986. Australian waterfowl do not necessarily breed on a rising water level. *Australian Wildlife Research* **13**, 461-80.

Crome F. H. J. and Carpenter S. M. 1988. Plankton community cycling and recovery after drought - dynamics in a basin on a floodplain. *Hydrobiologia* **164**, 193-211.

Crook D. A., Robertson A. I., King A. J. and Humphries P. 2001. The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river

fishes. *Oecologia* **129**, 525-33.

Crowley P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics* **23**, 405-47.

Cushing D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**, 249-93.

Dettmers J. M., Wahl D. H., Soluk D. A. and Gutreuter S. 2001. Life in the fast lane: fish and foodweb structure in the main channel of large rivers. *Journal of the North American Benthological Society* **20**, 255-65.

Diana J. S. 1995. Chapter 8: Density dependence, density independence, and the critical period. *In.* Diana J. S. (Ed.). *Biology and Ecology of Fishes*. Biological Sciences Press. Indiana, USA. pp 137-162.

DNRE. 1998. *Ovens Basin Water Quality Strategy* . Department of Natural Resources and Environment, Victoria, Shepparton, Australia.

DNRE. 1999. *Threatened Vertebrate Fauna in Victoria – 1999*. Department of Natural Resources and Environment. Melbourne, Australia.

Doherty P. Kingsford M., Booth D. and Carleton J. 1996. Habitat selection before settlement by *Pomacentrus coelestis*. *Marine and Freshwater Research* **47**, 391-9.

DWR. 1989a. *Water Victoria: An Environmental Handbook*. Victorian Government Publishing Office, Department of Water Resources, Melbourne, Australia.

DWR. 1989b. *Water Victoria: A Resource Handbook*. Victorian Government Publishing Office, Melbourne, Australia.

Dynesius M. and Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**, 753-62.

Edwards E. D. and Huryn A. D. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* **337**, 151-9.

Eklöv A. G., Greenberg L. A. and Kristiansen H. 1994. The effect of depth on the interaction between perch (*Perca fluviatilis*) and minnow (*Phoxinus phoxinus*).

Ecology of Freshwater Fish **3**, 1-8.

Emery A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *Journal of Fisheries Research Board Canada* **30**, 761-74.

Faragher R. A. and Harris J. H. 1994. The historical and current status of freshwater fish in New South Wales. *Australian Zoologist* **29**, 166-76.

Fernandes C. C. 1997. Lateral migration of fishes in Amazonian floodplains. *Ecology of Freshwater Fish* **6**, 36-44.

Ferrari I., Farabegoli A. and Mazzoni R. 1989. Abundance and diversity of planktonic rotifers in the Po River. *Hydrobiologia* **186/187**, 201-8.

Finger T. R. and Stewart E. M. 1987. Response of fishes to flooding regime in lowland hardwood wetlands. *In.* Matthews W. J. and Heins D. C. (Eds.). *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press. Norman, USA. pp 86-92.

Flore L. and Keckis H. 1998. The effect of water current on foraging behaviour of the rheophilic cyprinid *Chondrostoma nasus* (L.) during ontogeny: Evidence of a trade-off between energetic gain and swimming costs. *Regulated Rivers: Research and Management* **14**, 141-54.

Fontenot Q. C., Rutherford D. A. and Kelso W. E. 2001. Effects of environmental hypoxia associated with the annual flood pulse on the distribution of larval sunfish and shad in the Atchafalaya River Basin, Louisiana. *Transactions of the American Fisheries Society* **130**, 107-116.

Fortier L. and Gagné J. A. 1990. Larval herring (*Clupea harengus*) dispersion, growth and survival in the St. Lawrence estuary: match/mismatch or membership/vagrancy? *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1898-912.

Fuiman L. A. and Higgs D. M. 1997. Chapter 8: Ontogeny, growth and the recruitment process. *In.* Chambers R. C. and Trippel E. A. (Eds.). *Early Life History and Recruitment in Fish Populations*. Chapman and Hall. London, UK. pp 225-50.

Galat D. L., Fredrickson L. H., Humburg D. D., Bataille K. J., Bodie J. R., Dohrenwend J.,

Gelwicks G. T., Havel J. E., Helmers D. L., Hooker J. B., Jones J. R., Knowlton M. F., Kubisiak J., Mazourek J., McColpin A. C., Renken R. B. and Semlitsch R. D. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* **48**, 721-33.

Garcia-Berthou E. 1999. Food of introduced mosquitofish: ontogenetic diet shift and prey selection. *Journal of Fish Biology* **55**, 135-47.

Garman G. C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. *Environmental Biology of Fishes* **30**, 325-31.

Garner P. 1996. Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the river Great Ouse, England. *Journal of Fish Biology* **48**, 367-82.

Garner P. 1997. Sample sizes for length and density estimation of 0+ fish when using point sampling by electrofishing. *Journal of Fish Biology* **50**, 95-106.

Garner P., Clough S., Griffiths S. W., Deans D. and Ibbotson A. 1998. Use of shallow marginal habitat by *Phoxinus phoxinus*: a trade-off between temperature and food? *Journal of Fish Biology* **52**, 600-9.

Geddes M. C. and Puckridge J. T. 1988. Survival and growth of larval and juvenile native fish. The importance of the floodplain. *In.* Lawrence B. (Ed.). *Proceedings of the Native Fish Management Workshop*. Murray Darling Basin Commission. Canberra, Australia. pp 101-15.

Gehrke P. C. 1990a. Spatial and temporal dispersion patterns of golden perch, *Macquaria ambigua*, larvae in an artificial floodplain environment. *Journal of Fish Biology* **37**, 225-36.

Gehrke P. C. 1990b. Clinotactic responses of larval silver perch (*Bidyanus bidyanus)* and golden perch (*Macquaria ambigua)* to simulated environmental gradients. *Australian Journal of Marine and Freshwater Research* **41**, 523-8.

Gehrke P. C. 1991. Avoidance of inundated floodplain habitat by larvae of golden perch (*Macquaria ambigua* Richardson): Influence of water quality or food distribution? *Australian Journal of Marine and Freshwater Research* **42**, 707-19.

Gehrke P. C. 1992. Diel abundance, migration and feeding of fish larvae (Eleotridae) in a floodplain billabong. *Journal of Fish Biology* **40**, 695-707.

Gehrke P. C. 1993. Enhancing recruitment of native fish in inland environments by accessing alienated floodplain habitats. *In.* Hancock D. A. (Ed.). *Recruitment Processes. Proceedings of an Australian Society for Fish Biology Workshop (No. 16), Hobart, 21 August 1991.* Australian Government Publishing Service. Canberra, Australia. pp 205-9.

Gehrke P. C. 2001. The Paroo River. *In.* Young W. J. (Ed.). *Rivers as Ecological Systems: The Murray-Darling Basin.* Murray Darling Basin Commission. Canberra, Australia. pp 119-31.

Gehrke P. C., Revell M. B. and Philbey A. W. 1993. Effects of river red gum, *Eucalyptus camaldulensis,* litter on golden perch, *Macquaria ambigua. Journal of Fish Biology* **43**, 265-79.

Gehrke P. C. and Harris J. H. 2000. Large-scale patterns in species richness and composition of temperate riverine fish communities. south-eastern Australia. *Marine and Freshwater Research,* **51**, 165-82.

Gerking S. D. 1994. Chapter 7: Larval Feeding. *In.* Gerking S. D. (Ed.). *Feeding Ecology of Fish.* Academic Press. San Diego, USA. pp 139-70.

Gotceitas V., Puvanendran V., Leader L. L. and Brown J. A. 1996. An experimental investigation of the 'match/mismatch' hypothesis using larval Atlantic cod. *Marine Ecology Progress Series* **130**, 29-37.

Goulding M. 1980. *The Fishes and the Forest. Explorations in Amazonian Natural History.* University of California Press, Berkeley, USA.

Gozlan R. E., Mastrorillo S., Dauba F., Tourenq J. and Copp G. H. 1998. Multi-scale analysis of habitat use during late summer for 0+ fishes in the River Garonne (France). *Aquatic Sciences* **60**, 99-117.

Gutreuter S., Bartels A.D., Irons K. and Sandheinrich, M.B. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper

Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2282-91.

GWQWG. 1996. *Draft Goulburn Broken Catchment Water Quality Strategy*. Goulburn Water Quality Working Group, Shepparton, Australia.

Haines G. B. and Tyus H. M. 1990. Fish associations and environmental variables in age-0 Colorado squawfish habitats, Green River, Utah. *Journal of Freshwater Ecology* **5**, 427-35.

Hakenkamp C. C. and Morin A. 2000. The importance of meiofauna to lotic ecosystem functioning. *Freshwater Biology* **44**, 165-75.

Halyk L. C. and Balon E. K. 1983. Structure and ecological production of the fish taxocene of a small floodplain system. *Canadian Journal of Zoology* **61**, 2446-64.

Harris J. H. 1984. Zoogeography of the Australian freshwater fish fauna. *In.* Archer M and Clayton G. (Eds.). *Vertebrate Zoogeography and Evolution in Australasia.* Hesperian Press. Perth, Australia. pp 211-22.

Harris J. H. and Gehrke P. C. 1994. Modelling the relationship between streamflow and population recruitment to manage freshwater fisheries. *Agricultural Systems and Information Technology* **6**, 28-30.

Harris J. H. and Rowland S. J. 1996. Family Percichthyidae: Australian Freshwater Cods and Basses. *In* McDowall R. M. (Ed.). *Freshwater Fishes of South-Eastern Australia.* Reed Books. Sydney, Australia. pp 150-63.

Harrison J., Schalken A., Rankin T. and Croome R. 1990. *Lake Mokoan and the Broken River: Factors Affecting Water Quality.* Rural Water Commission of Victoria, Melbourne, Australia.

Harvey B. C 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Oecologia* **87**, 29-36.

Harvey B. C. and Stewart A. J. 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia* **87**, 336-42.

Hawking J. and Smith F. 1997. *Colour Guide to Invertebrates of Australian Inland Waters*. Cooperative Research Centre for Freshwater Ecology, Albury, Australia.

Hayes D. B., Ferreri C. P. and Taylor W. W. 1996. Active fish capture methods. *In.* Murphy B. R. and Willis D. W. (Eds.). *Fisheries Techniques*. American Fisheries Society. Bethesda, Marysland, USA. pp 193-220.

Hill T. J. and Willis D. W. 1994. Influence of water conductivity in pulsed AC and pulsed DC electrofishing catches for largemouth bass. *North American Journal of Fisheries Management* **14**, 202-7.

Hjort J. 1914. Fluctuations in the Great Fisheries of Northern Europe viewed in the light of biological research. *Rapports et Procés-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer* **20**, 1-220.

Houde E. D. 1987. Fish early life history dynamics and recruitment variability. *American Fisheries Society Symposium* **2**, 17-29.

Houde E. D. 1997. Chapter 6: Patterns and consequences of selective processes in teleost early life histories. *In.* Chambers R. C. and Trippel E. A. (Eds.). *Early Life History and Recruitment in Fish Populations*. Chapman and Hall. London. pp 173-96.

Hughes R. N. 1997. Diet selection. *In.* Godin J. G. J. (Ed.). *Behavioural Ecology of Teleost Fishes*. Oxford University Press. New York, USA. pp 134-62.

Hume D. H., Fletcher A. R. and Morison A. K. 1983. *Final Report. Carp Program Report No. 10*. Fisheries and Wildlife Division, Victorian Ministry for Conservation, Melbourne, Australia.

Humphries P 1995. Life history, food and habitat of southern pygmy perch, *Nannoperca australis*, in the Macquarie River, Tasmania. *Marine and Freshwater Research* **46**, 1159-69.

Humphries P., King A. J. and Koehn J. D. 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes* **56**, 129-51.

Humphries P. and Lake P. S. 2000. Fish larvae and the management of regulated rivers.

Regulated Rivers: Research and Management **16**, 421-32.

Humphries P., Serafini L. and King A. J. In Press. River regulation and fish larvae: variations through space and time. *Freshwater Biology.*

Hyndes G. A., Platell M. E. and Potter I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. *Marine Biology* **128**, 585-98.

Hynes H. B. N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* **19**, 36-58.

Hyslop E. J. 1980. Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology* **17**, 411-29.

Ingram B. A. and Rimmer M. A. 1992. Induced breeding and larval rearing of the endangered Australian freshwater fish trout cod, *Maccullochella macquariensis* (Cuvier) (Percichthyidae). *Aquaculture and Fisheries Management* **24**, 7-17.

Ingram B. A. and Douglas J. W. 1995. Threatened fishes of the world: *Maccullochella macquariensis* (Cuvier, 1829) (Percichthyidae). *Environmental Biology of Fishes* **43**, 38.

Jackson P. D. 1978. Spawning and early development of the river blackfish, *Gadopsis marmoratus* Richardson (Gadopsiformes: Gadopsidae), in the McKenzie River, Victoria. *Australian Journal of Marine and Freshwater Research* **29**, 293-8.

Jobling M. 1995. *Environmental Biology of Fishes.* Chapman and Hall Publishers, London, UK.

Junk W. J. and Welcomme R. L. 1990. Floodplains. *In.* Patten B. C. (Ed.). *Wetlands and Shallow Continental Water Bodies.* SPB Academic Publishing. The Hague, Netherlands. pp 491-524.

Junk W. J., Bayley P. B. and Sparks R. E. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**, 110-27.

Juradja P. 1998. Drift of larval and juvenile fishes, especially *Rhodeus sericeus* and *Rutilus rutilus*, in the River Morava (Danube basin). *Archiv für Hydrobiologie* **141**, 231-41.

Jurajda P. 1999. Comparative nursery habitat use by 0+ fish in a modified lowland river. *Regulated Rivers: Research and Management* **15**, 113-24.

Keast A., Harker J. and Turnbull D. 1978. Nearshore fish habitat utilisation and species associations in Lake Opinicon (Ontario, Canada). *Environmental Biology of Fishes* **3**, 173-84.

Kelso W. E. and Rutherford D. A. 1996. Collection, preservation and identification of fish eggs and larvae. *In.* Murphy B. R. and Willis D. W. (Eds.). *Fisheries Techniques.* American Fisheries Society. Bethesda, Marysland, USA. pp 255-302.

Kennard M., Pusey B. and Arthington A. 2001. *Trophic Ecology of Freshwater Fishes in Australia.* Cooperative Research Centre for Freshwater Ecology, Brisbane, Australia.

Killgore K. J. and Baker J. A. 1996. Patterns of larval fish abundance in a bottomland hardwood wetland. *Wetlands* **16**, 288-95.

Kobayashi T., Shiel R. J., Gibbs P. and Dixon P. I. 1998. Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. *Hydrobiologia* **377**, 133-45.

Koehn J. D. 1986. Approaches to determining flow and habitat requirements for freshwater native fish in Victoria. *In.* Campbell I. C. (Ed.). *Stream Protection - The Management of Rivers for Instream Uses.* Water Studies Centre, Chisholm Institute. Melbourne, Australia. pp 95-113.

Koehn J. D. 1997. Habitats and movements of freshwater fish in the Murray-Darling Basin. *In.* Banens R. J. and Lehane R. (Eds.). *1995 Riverine Environment Research Forum, 4 - 6 October 1995.* Murray-Darling Basin Commission. Canberra, Australia. pp 27-32.

Koehn J. D. and O'Connor W. G. 1990a. Threats to Victorian native freshwater fish.

Victorian Naturalist **107**, 5-12.

Koehn J. D. and O'Connor W. G. 1990b. *Biological Information for Management of Native Freshwater Fish in Victoria*. Victorian Government Printing Office, Melbourne, Australia.

Koehn J. D., Brumley A. and Gehrke P. C. 2000. *Managing the Impacts of Carp*. Bureau of Rural Sciences, Department of Agriculture, Fisheries and Forestry, Canberra, Australia.

Kramer D. L., Rangeley R. W. and Chapman L. J. 1997. Habitat selection: patterns of spatial distribution from behavioural decisions. *In.* Godin J. J. (Ed.). *Behavioral Ecology of Teleost Fishes*. Oxford University Press. Oxford, UK. pp 37-80.

Lake J. S. 1967a. Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Australian Journal of Marine and Freshwater Research* **18**, 137-53.

Lake J. S. 1967b. Rearing experiments with five species of Australian freshwater fishes. II. Morphogenesis and ontogeny. *Australian Journal of Marine and Freshwater Research* **18**, 155-73.

Lake J. S. 1971. *Freshwater Fishes and Rivers of Australia.* Thomas Nelson and Sons Ltd, Melbourne, Australia.

Lake P. S. 1995. Of floods and droughts: river and stream ecosystems of Australia. *In* Cushing C. E., Cummins K. W. and Minshall G. W. (Eds.). *River and Stream Ecosystems. Ecosystems of the World 22*. Elsevier. Amsterdam. pp 659-94.

Langler G. J. and Smith C. 2001. Effects of habitat enhancement of 0-group fishes in a lowland river. *Regulated Rivers: Research and Management* **17**, 677-86.

Larson H. K. and Hoese D. F. 1996. Family Gobiidae, subfamilies Eleotridinae and Butinae: Gudgeons *In* McDowall, R. M. (Ed.). Freshwater Fishes of South-eastern Australia. Reed Books, Sydney, Australia. pp. 200-28.

Leis J. M. 1991. Chapter 8: The pelagic stage of reef fishes: the larval biology of coral reef fishes. *In.* Sale P. F. (Ed.). *The Ecology of Coral Reef Fishes*. Academic Press.

California, USA. pp 183-230.

Leis J. M. and Carson-Ewart B. M. 1998. Complex behaviour by coral-reef fish larvae in open-water and near-reef pelagic environments. *Environmental Biology of Fishes* **53**, 259-66.

Lewis M. 1970. Morphological adaptations of cyprinodontoids for inhabiting oxygen-deficient waters. *Copeia* **1970**, 319-26.

Li H. W. and Moyle P. B. 1993. Management of introduced fishes. *In.* Kohler C. C. and Hubert W. A. (Eds.). *Inland Fisheries Management in North America.* American Fisheries Society. Bethesda, Maryland, USA. pp 287-307.

Lieschke J. A. and Closs G. P. 1999. Regulation of zooplankton composition and distribution by a zooplanktivorous fish in a shallow, eutrophic floodplain lake in south east Australia. *Archiv für Hydrobiologie* **146**, 397-412.

Lightfoot G. W. and Jones N. V. 1996. The relationship between the size of 0+ roach, *Rutilus rutilus,* their swimming capabilities, and distribution in an English river. *Folia Zoologica* **45**, 355-60.

Llewellyn L. C. 1971. Breeding studies on the freshwater forage fish of the Murray-Darling river system. *The Fisherman* 1-12.

Llewellyn L. C. 1973. Spawning, development and temperature tolerance of the spangled perch *Madigania unicolor* (Günther) from inland waters in Australia. *Australian Journal of Marine and Freshwater Research* **25**, 121-49.

Llewellyn L. C. 1974. Spawning, development and distribution of the southern pygmy perch *Nannoperca australis* Günther from inland waters in Eastern Australia. *Australian Journal of Marine and Freshwater Research* **25**, 121-49.

Llewellyn L.C. 1979. Some observations on the sawning and dvelopment of the Mitchellian freshwater hardyhead *Craterocephalus fluviatilis* McCulloch from inland water in New South Wales. *Australian Zoologist* **20**, 269-99.

Lloyd L. N. 1987. *Ecology and distribution of small native fish of the lower River Murray, South Australia and their interactions with exotic mosquitofish, Gambusia affinis*

holbrooki (Girard). University of Adelaide, South Australia. MSc Thesis.

Lloyd L. N. and Walker K. F. 1986. Distribution and conservation status of small freshwater fish in the River Murray, South Australia. *Transactions Royal Society of South Australia* **110**, 49-57.

Lloyd L., Puckridge J. and Walker K. 1989. The significance of fish populations in the Murray-Darling system and their requirements for survival. *In.* Dendy T and Coombe M. (Eds.). *Conservation in Management of the River Murray System - Making Conservation Count. Proceedings of the Third Fenner Conference on the Environment, Canberra. September 1989.* Australian Academy of Science, South Australian Department of Environment and Planning. Adelaide, Australia. pp 86-99.

Lloyd L., Atkins B., Boon P., Jacobs T. and Roberts J. 1994. Natural processes within Murray-Darling floodplain wetlands. *In.* Sharley T. and Huggan C. (Eds.). *Murray-Darling Basin Floodplain Wetlands Management. Proceedings of the Floodplain Wetlands Management Workshop.* Murray Darling Basin Commission. Canberra, Australia. pp 6-23.

Lowe-McConnell R. H. 1975. *Fish Communities in Tropical Freshwaters.* Longman, London, UK.

Mackay N. J. 1973. Histological changes in the ovaries of the golden perch, *Plectroplites ambiguus,* associated with the reproductive cycle. *Australian Journal of Marine and Freshwater Research* **24**, 95-101.

MacNally R. C. 1995. *Ecological Versatility and Community Ecology.* Cambridge University Press, New York, USA.

Maheshwari B. L., Walker K. F. and McMahon T. A. 1995. Effects of regulation on the flow regime of the River Murray, Australia. *Regulated Rivers: Research and Management* **10**, 15-38.

Mallen-Cooper M., Stuart I. G., Hides-Pearson R. and Harris J. H. 1995. *Fish Migrations in the Murray River and Assessment of the Torrumbarry Fishway.* NSW Fisheries, Sydney, Australia.

Mann R. H. K. and Bass J. A. B. 1997. The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management. *Regulated Rivers: Research and Management* **13**, 295-301.

Mann R. H. K., Bass J. A. B., Leach D. and Pinder A. C. 1997. Temporal and spatial variations in the diet of 0 group roach (*Rutilus rutilus (L.)*) larvae and juveniles in the River Great Ouse in relation to prey availability. *Regulated Rivers: Research and Management* **13**, 287-94.

Mark W., Hofer R. and Wieser W. 1987. Diet spectra and resource partitioning in the larvae and juveniles of three species and six cohorts of cyprinids from a subalpine lake. *Oecologia* **71**, 388-96.

Mark W., Wieser W. and Hohenauer C. 1989. Interactions between developmental processes, growth, and food selection in the larvae and juveniles of *Rutilus rutilus* (L.) (Cyprinidae). *Oecologia* **78**, 330-7.

Mathur D. 1977. Food habitats and competitive relationships of the bandfin shiner in Halawakee Creek, Alabama. *American Midland Naturalist* **97**, 89-100.

May R. C. 1974. Larval mortality in fishes. *In.* Blaxter J. H. S. (Ed.). *The Early Life History of Fish*. Springer-Verlag. Berlin, Germany. pp 3-19.

McCune B. and Mefford M. J. 1999. *PC-ORD Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Oregon, USA.

McDowall R. M. (Ed.). 1996. *Freshwater Fishes of South-Eastern Australia*. 2nd edition. Reed Books, Sydney, Australia.

McKinnon L. J. 1997. *Monitoring of Fish Aspects of the Flooding of Barmah Forest*. Marine and Freshwater Resources Institute, Queenscliff, Australia.

Meng L. 1993. Sustainable swimming speeds of striped bass larvae. *Transactions of the American Fisheries Society* **122**, 702-8.

Mérigoux S. and Ponton D. 1998. Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America. *Journal of Fish Biology* **52**, 556-69.

Merrit R. W. and Cummins K. W. (Eds.). 1984. *An Introduction to the Aquatic Insects of North America*. 2nd edition. Kendall Hunt Publishing Company, Iowa, USA.

Miller T. J., Crowder L. B., Rice. J. A. and Marschall E. A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1657-70.

Milton D. A. and Arthington A. H. 1983. Reproduction and growth of *Craterocephalus marjoriae* and *C. stercusmuscarum* (Pisces: Atherinidae) in south-eastern Queensland, Australia. *Freshwater Biology* **13**, 589-97.

Milton D. A. and Arthington A. H. 1984. Reproductive strategy and growth of the crimson-spotted rainbowfish, *Melanotaenia splendida fluviatilis* (Castelnau) (Pisces: Melanotaeniidae) in South-eastern Queensland. *Australian Journal of Marine and Freshwater Research* **35**, 75-83.

Milton D. A. and Arthington A. H. 1985. Reproductive strategy and growth of the Australian smelt, *Retropinna semoni* (Weber) (Pisces: Retropinnidae), and the olive perchlet, *Ambassis nigripinnis* (De Vis) (Pisces: Ambassidae), in Brisbane, South-eastern Queensland. *Australian Journal of Marine and Freshwater Research* **36**, 329-41.

Mittelbach G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**, 1370-86.

Mittelbach G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**, 499-513.

Mol J. H. 1995. Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes. *Journal of Fish Biology* **47**, 788-807.

Moore K. M. S. and Gregory S. V. 1988a. Summer habitat utilization and ecology of Cutthroat Trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1921-30.

Moore K. M. S. and Gregory S. V. 1988b. Response of young-of-the-year cutthroat trout to manipulation of habitat structure in a small stream. *Transactions of the American*

Fisheries Society **117**, 162-70.

Nakano S., Miyasaka H. and Kuhara N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* **80**, 2435-41.

Neira F. J., Miskiewicz A. G. and Trnski T. 1998. *Larvae of Temperate Australian Fishes. Laboratory Guide for Larval Fish Identification.* University of Western Australian Press, Perth, Australia.

Nelva A., Persat H. and Chessel D. 1979. Une nouvelle méthode d'étude des peuplements ichtyologiques dans les grands cours d'eau par échantiollonnage ponctuel d'abondance. *Comptes Rendus Hebdomadaires des Seances de Academie des Sciences Paris* **289**, 1295-8.

Nicol S. J., Bearlin A. R., Robley A. J., Koehn J. D. and Lieschke J. A. 2001. Distribution of large woody debris in the mid-reaches of the Murray River. *Ecological Management and Restoration* **2**, 64-7.

Nix H. A. and Kalma J. D. 1982. The climate of the Murray-Darling Basin. *In.* CSIRO Division of Land and Water Resources. *Murray-Darling Basin Project Development Study, Stage 1, Working Paper.* CSIRO Division of Land and Water Resources. Canberra, Australia.

O'Connor W. G. and Koehn J. D. 1991. Spawning of the mountain galaxias, *Galaxias olidus* Günther, Bruces Creek, Victoria. *Proceedings of the Royal Society of Victoria* **103**, 113-23.

Odum H. T. and Caldwell D. K. 1955. Fish respiration in the natural oxygen gradient of an anaerobic spring in Florida. *Copeia* **1955**, 104-6.

Öhman M. C., Munday P. L., Jones G. P. and Caley M. J. 1998. Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology* **225**, 219-38.

Olson M. H. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. *Ecology* **77**, 179-90.

Osenberg C. W., Olson M. H., Mittelbach G. G. 1994. Stage structure in fishes: resource

productivity and competition gradients. *In.* Stouder D. J., Fresh K. L. and Feller R. J. (Eds.). *Theory and Application of Fish Feeding Ecology*. University of South Carolina Press. South Carolina, USA. pp 51-70.

Ott M. E., Heisler N. and Ultish G. R. 1980. A re-evaluation of the relationship between temperature and the critical oxygen tension in freshwater fishes. *Comparative Biochemistry and Physiology* **67A**, 337-40.

Pace M. L., Findlay S. E. and Lints D. 1992. Zooplankton in advective environments: The Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1060-9.

Paine M. D. 1984. Ecological and evolutionary consequences of early ontogenies of darter (Etheostomatini). *Environmental Biology of Fishes* **11**, 97-106.

Paller M. H. 1987. Distribution of larval fish between macrophyte beds and open channels in a southeastern floodplain swamp. *Journal of Freshwater Ecology* **4**, 191-200.

Panek F. M. 1987. Biology and ecology of carp. *In.* Cooper E. L. (Ed.). *Carp in North America*. American Fisheries Society. Bethesda, Marysland, USA. pp 1-15.

Pearsons T. N., Hiram W. L. and Lamberti G. A. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society* **121**, 427-36.

Pen L. J. and Potter I. C. 1991. Reproduction, growth and diet of *Gambusia holbrooki* (Girard) in a temperate Australian river. *Aquatic Conservation: Marine and Freshwater Ecosystems* **1**, 159-72.

Pen L. J., Potter I. C. and Calver M. C. 1993. Comparisons of the food niches of three native and two introduced fish species in an Australian river. *Environmental Biology of Fishes* **36**, 167-82.

Persson L. 1987a. The effects of resource availability and distribution on size class interactions in perch *Perca fluviatilis*. *Oikos* **48**, 148-60.

Persson L. 1987b. The effects of habitat and season on competitive interactions between roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*). *Oecologia* **73**, 170-7.

Persson L. and Greenberg L. A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) - roach (*Rutilus rutilus*) interaction. *Ecology* **71**, 44-56.

Pianka E. R. 1986. *Ecology and Natural History of Desert Lizards.* Princeton University Press, New Jersey, USA.

Pielou E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* **10**, 370-83.

Poff N. E. and Allan J. D. 1995. Functional organisation of stream fish assemblages in relation to hydrological variability. *Ecology* **76**, 606-27.

Poff N. L., Allan J. D., Bain M. B., Karr J. R., Prestegaard K. L., Richter B. D., Sparks R. E. and Stromberg J. C. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* **47**, 769-84.

Poizat G. and Pont D. 1996. Multi-scale approach to species-habitat relationships: juveniie fish in a large river section. *Freshwater Biology* **36**, 611-22.

Poizat G. and Crivelli A. J. 1997. Use of seasonally flooded marshes by fish in a Mediterranean wetland: timing and demographic consequences. *Journal of Fish Biology* **51**, 106-119.

Potvin C. and Roff D. A. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* **74**, 1617-28.

Power M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. *In.* Kerfoot W. C. and Sih A. (Eds.). *Predation: Direct and Indirect Impacts on Aquatic Communities.* University of New England. New Hampshire, USA. pp 333-51.

Power M. E., Dudley T. and Cooper S. 1989. Grazing catfish, fishing birds and attached algae in a Panamanian stream. *Environmental Biology of Fishes* **26**, 285-94.

Puckridge J. T., Sheldon F., Walker K. F. and Boulton A. J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**, 55-72.

Pusey B. J., Arthington A. H. and Read M. G. 2000. The dry-season diet of freshwater

fishes in monsoonal tropical rivers of Cape York Peninsula, Australia *Ecology of Freshwater Fish* **9**, 177-90.

Quinn G. P, Hillman T. J. and Cook R. A. 2000. The response of macroinvertebrates to inundation in floodplain wetlands: a possible effect of river regulation ? *Regulated Rivers: Research and Management* **16**, 469-77.

Reckendorfer W., Heckeis H., Winkler G. and Schiemer F. 1999. Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. *Freshwater Biology* **41**, 583-91.

Regis J., Pattée E. and Lebreton J. D. 1981. A new method for evaluating the efficiency of electric fishing. *Archiv für Hydrobiologie* **93**, 68-82.

Reid D. D., Harris J H and Chapman D. J. 1997. *NSW Inland Commercial Fishery Data Analysis*. NSW Fisheries, Sydney, Australia.

Reynolds C. S. 2000. Hydroecology of river plankton: the role of variability in channel flow. *Hydrological Processes* **14**, 3119-32.

Reynolds J. B. 1996. Electrofishing. *In.* Murphy B. R. and Willis D. W. (Eds.). *Fisheries Techniques*. American Fisheries Society. Bethesda, Marysland, USA. pp 221-53.

Reynolds L. F. 1983. Migration patterns of five fish species in the Murray-Darling river system. *Australian Journal of Marine and Freshwater Research* **34**, 857-71.

Rheinberger V., Hofer R. and Wieser W. 1987. Growth and habitat separation in eight cohorts of three species of cyprinids in a subalpine lake. *Environmental Biology of Fishes* **18**, 209-17.

Rincón P. A., Barrachina P. and Bernat Y. 1992. Microhabitat use by 0+ juvenile cyprinids during summer in a Mediterranean river. *Archiv für Hydrobiologie* **125**, 323-37.

Robertson A. L. 1990. The population dynamics of Chydoridae and Macrothricidae (Cladocera: Crustacea) from the River Thames, U.K. *Freshwater Biology* **24**, 375-89.

Robertson A. L. 2000. Lotic meiofaunal community dynamics: colonisation, resilience and persistence in a spatially and temporally heterogeneous environment. *Freshwater Biology* **44**, 135-47.

Robertson A. L., Lancaster J. and Hildrew A. G. 1995. Stream hydraulics and the distribution of microcrustacea: role for refugia ? *Freshwater Biology* **33**, 469-84.

Robertson A. L., Lancaster J., Belyea L. R. and Hildrew A. G. 1997. Hydraulic habitat and the assemblage structure of stream benthic microcrustacea. *Journal of the North American Benthological Society* **16**, 562-75.

Robertson A. L., Rundle S. D. and Schmid-Araya J. M. 2000a. An introduction to a special issue on lotic meiofauna. *Freshwater Biology* **44**, 1-3.

Robertson A. L., Rundle S. D. and Schmid-Araya J. M. 2000b. Putting the meio- into stream ecology: current findings and future directions for lotic meiofaunal research. *Freshwater Biology* **44**, 177-83.

Ross S. T. and Baker J. A. 1983. The response of fishes to periodic spring floods in a southeastern stream. *The American Midland Naturalist* **109**, 1-14.

Rowland S. J. 1983. Spawning of the Australian freshwater fish Murray cod, *Maccullochella peeli* (Mitchell), in earthen ponds. *Journal of Fish Biology* **23**, 525-34.

Rowland S. J. 1992. Diet and feeding of Murray Cod *(Maccullochella peelii)* larvae. *Proceedings of the Linnean Society of New South Wales* **113**, 193-201.

Rundle A. S. and Rowe R. K. 1974. *A Study of the Land in the Catchment of the Broken River*. Soil Conservation Service, Melbourne, Australia.

Rundle S. D. and Hildrew A. G. 1992. Small fish and small prey in the food webs of some southern English streams. *Archiv für Hydrobiologie* **125**, 25-35.

Sadzikowski M. R. and Wallace D. C. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* (L.) and *L. cyanellus* Rafinesque). *American Midland Naturalist* **95**, 220-5.

Schael D. M., Rudstam. L. G. and Post J. R 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1919-25.

Schiemer F. and Spindler T. 1989. Endangered fish species of the Danube River in Austria. *Regulated Rivers: Research and Management* **4**, 397-407.

Schiemer F., Spindler T., Wintersberger H., Schneider A. and Chovanec A. 1991. Fish fry associations: Important indicators for the ecological status of large rivers. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **24**, 2497-500.

Schiller C. B. and Harris J. H. 2001. Chapter 6: Native and alien fish. *In.* Young W. J. (Ed.). *Rivers as Ecological Systems: The Murray-Darling Basin.* Murray Darling Basin Commission. Canberra, Australia. pp 229-58.

Schindler D. W. 1969. Two useful devices for vertical plankton and water sampling. *Journal of Fisheries Research Board of Canada* **26**, 1948-55.

Schlosser I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* **68**, 651-9.

Schmid-Araya J. M. and Schmid P. E. 2000. Trophic relationships: integrating meiofauna into a realistic benthic food web. *Freshwater Biology* **44**, 149-63.

Schoener T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408-18.

Scott M. T. and Nielsen L. A. 1989. Young fish distribution in backwaters and main-channel borders of the Kanawha River, West Virginia. *Journal of Fish Biology* **35** (Supp. A), 21-7.

Scrimgeour G. J. and Winterbourn M. J. 1987. Diet, food resource partitioning and feeding periodicity of two riffle-dwelling fish species in a New Zealand river. *Journal of Fish Biology* **31**, 309-24.

Sempeski P. and Gaudin P. 1995. Size-related changes in diel distribution of young

grayling (*Thymallus thymallus*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1842-8.

Shelbourne J. E. 1962. A predator-prey size relationship for plaice larvae feeding on *Oikopleura*. *Journal of the Marine Biological Association of the United Kingdom* **42**, 243-52.

Shiel R. J. 1985. Zooplankton of the Darling River system, Australia. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **22**, 2136-40.

Shiel R. J. 1995. *A Guide to the Identification of Rotifers, Cladocerans and Copepods from Australian Inland Waters*. Cooperative Research Centre for Freshwater Ecology, Albury, Australia.

Shiel R. J., Walker K. F. and Williams W. D. 1982. Plankton of the Lower River Murray, South Australia. *Australian Journal of Marine and Freshwater Research* **33**, 301-27.

Shiozawa D. K. 1991. Microcrustacea from the benthos of nine Minnesota streams. *Journal of the North American Benthological Society* **10**, 286-99.

Snyder D. E. 1976. Terminologies for intervals of larval fish development. *In.* Boreman J. (Ed.). *Great Lakes Fish Egg and Larvae Identification (Proceedings of a Workshop)*. US Fish and Wildlife Service, National Power Plant Team. Ann Arbour, Michigan, USA. pp 41-60.

Sokal R. R. and Rohlf F. J. 1995. *Biometry*. 3rd Edition. W.H. Freeman and Company, New York, USA.

Sparks R. E. 1995. Need for ecosystem management of large rivers and their floodplains. *BioScience* **45**, 168-82.

Sparks R. E., Bayley P. B., Kohler S. L. and Osborne L. L. 1990. Disturbance and recovery of large floodplain rivers. *Environmental Management* **14**, 699-709.

Sparks R. E., Nelson J. C. and Yin Y. 1998. Naturalisation of the flood regime in regulated rivers. *BioScience* **48**, 706-20.

SPSS Inc. 1997. *SigmaPlot for Windows, Version 4*. SPSS Inc., USA

Stanford J. A., Ward J. V., Liss W. J., Frissell C. A., Williams R. N., Lichatowich J. A. and Coutant C. C. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* **12**, 391-413.

Tan L. and Shiel R. J. 1993. Responses of billabong rotifer communities to inundation. *Hydrobiologia* **255/256**, 361-9.

Thoms M. C. and Sheldon F. 2000. Lowland rivers: an Australian introduction. *Regulated Rivers: Research and Management* **16**, 375-83.

Thorp J. H. and Covich A. P. (Eds.) 1991. *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, London, UK.

Thorp J. H. and Delong M. D. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**, 305-8.

Thorp J. H., Black A. R., Haag K. H. and Wehr J. D. 1994. Zooplankton assemblages in the Ohio River: Seasonal, tributary, and navigation dam effects. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1634-43.

Thorp J. H., Delong M. D., Greenwood K. S. and Casper A. S. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia* **117**, 551-63.

Tockner K., Malard F. and Ward J. V. 2000. An extension of the flood pulse concept. *Hydrological processes* **14**, 2861-83.

Trippel E. A. and Chambers R. C. 1997. The early life history of fishes and its role in recruitment processes. *In.* Chambers R. C. and Trippel E. A. (Eds.). *Early Life History and Recruitment in Fish Populations*. Chapman and Hall. London, UK. pp 21-32.

Turner T. F., Trexler J. C., Miller G. L. and Toyer K. E. 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia* **1994**, 174-83.

Tyus H. M. 1991. Movements and habitat use of young Colorado squawfish in the Green River, Utah. *Journal of Freshwater Ecology* **6**, 43-51.

Vannote R. L., Marshall G., Cummins K. W., Sedell J. R. and Cushing C. E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-7.

Velho L. F. M., Lansac-Tohu F. A. and Bini L. M. 1999. Spatial and temporal variation in densities of testate amoebae in the plankton of the Upper Parana River floodplain, Brazil. *Hydrobiologia* **411**, 103-13.

Villizzi L. 1998. Observations on ontogenetic shifts in the diet of 0+ carp, *Cyprinus carpio*, from the River Murray, Australia. *Folia Zoologica* **47**, 225-9.

Walker K. F. 1979. Regulated streams in Australia: The Murray-Darling river system. *In.* Ward J. V. and Standford J. A. (Eds.). *The Ecology of Regulated Streams*. Plenum Press. New York, USA. 143-63.

Walker K. F. 1992. A semi-arid lowland river: the River Murray, Australia. *In.* Calow P. A. and Petts G. E. (Eds.). *The Rivers Handbook, Volume 1*. Blackwell Scientific. Oxford, UK. pp 472-92.

Walker K. F. and Thoms M. C. 1993. Environmental effects of flow regulation on the lower River Murray, Australia. *Regulated Rivers: Research and Management* **8**, 103-19.

Walker K F., Sheldon F. and Puckridge J. T. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management* **11**, 85-104.

Wallace R. K. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* **110**, 72-6.

Ward J. V. and Stanford J. A. (Eds.). 1979. *The Ecology of Regulated Streams*. Plenum Press, New York, USA.

Ward J. V., Tockner K., Uehlinger U. and Malard F. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research and Management* **17**, 311-23.

Waters T. F. 1972. The drift of stream insects. *Annual Review of Entomology* **17**, 253-72.

Watkins M. S., Doherty S. and Copp G. H. 1997. Microhabitat use by 0+ and older fishes in a small English chalk stream. *Journal of Fish Biology* **50**, 1010-24.

Welcomme R. L. 1979. *Fisheries Ecology of Floodplain Rivers*. Longman, London, UK.

Welcomme R. L. 1985. *River Fisheries*. Food and Agriculture Organisation of the United Nations, FAO Fisheries Technical Paper 262, Rome, Italy.

Werner E. E. and Gilliam J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**, 393-425.

Werner E. E. and Hall, D. J. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology* **60**, 256-64.

Werner E. E. and Hall D. J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* **69**, 1352-66.

White R. J. 1996. Growth and development of North American stream habitat management for fish. *Canadian Journal of Fisheries and Aquatic Sciences* **53** (Suppl. 1), 342-63.

Whittington J. and Hillman T. J. 1999. *Sustainable Rivers: the Cap and Environmental Flows*. Cooperative Research Centre for Freshwater Ecology, Canberra, Australia.

Wilbur H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* **11**, 67-93.

Wilkinson L. 1990. *SYSTAT: The System for Statistics*. SYSTAT Inc., Illinois, USA.

Williams W. D. 1980. *Australian Freshwater Life. The Invertebrates of Australian Inland Waters*. Macmillan, Melbourne, Australia.

Winemiller K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* **26**, 177-99.

Winemiller K. O. 1992. Life-history strategies and the effectiveness of sexual selection. *Oikos* **63**, 318-27.

Winemiller K. O. and Rose K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196-218.

Winemiller K. O. and Rose K. A. 1993. Why do most fish produce so many tiny offspring? *The American Naturalist* **142**, 585-603.

Winkler G., Keckeis H., Reckendorfer W. and Schiemer F. 1997. Temporal and spatial dynamics of 0+ *Chondrostoma nasus*, at the inshore zone of a large river. *Folia Zoologica* **46**, 151-68.

Wintersberger H. 1996. Spatial resource utilization and species assemblages of larval and juvenile fishes. *Archiv für Hydrobiologie* (Suppl.) **115**, 29-44.

Wong B. and Ward F. J. 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. *Journal of the Fisheries Research Board of Canada* **29**, 1761-64.

Wooton R. J. 1998. *Ecology of Teleost Fishes*. 2nd edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Wu L. and Culver D. A. 1992. Ontogenetic diet shift in Lake Erie Age-0 yellow perch (*Perca flavescens*): A size-related response to zooplankton density. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1932-7.

Young W. J. 1999. Hydrological descriptions of semi-arid rivers: an ecological perspective. *In.* Kingsford R. T. (Ed.). *A Free-flowing River: the Ecology of the Paroo River*. NSW National Parks and Wildlife Service. Sydney, Australia. pp 77-96.

Young W. J. 2001. Landscapes, climates and flow regimes. *In.* Young W. J. (Ed.). *Rivers as Ecological Systems: The Murray-Darling Basin*. Murray-Darling Basin Commission. Canberra, Australia. pp 135-72.

Young W. J. and Hillman T. J. 2001. The Murray River - to the Darling River junction. *In.*

Young W. J. (Ed.). *Rivers as Ecological Systems: The Murray-Darling Basin.* Murray Darling Basin Commission. Canberra, Australia. pp 101-18.

Young W. J., Schiller C. B., Roberts J. and Hillman T. J. 2001. The rivers of the basin and how they work. *In.* Young W. J. (Ed.). *Rivers as Ecological Systems: The Murray-Darling Basin.* Murray-Darling Basin Commission. Canberra, Australia. pp 3-44.

Zaret T. M. and Rand A. S. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. *Ecology* **52**, 336-42.